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**An Assessment and Annotated  
Bibliography of Marine Bioluminescence  
Research: 1979-1987**

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*Ocean Sciences Branch  
Oceanography Division*

January 1993

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## Executive Summary

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# An Assessment and Annotated Bibliography of Marine Bioluminescence Research: 1979-1987

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## Introduction

Observations of bioluminescence at sea have been reported in scientific literature and in accounts of mariners at least since World War I (Tarasov, 1956). Questions concerning the distribution (seasonal and geographic) and variation of the bioluminescent field, signal intensity, spectrum, kinetics, and organism stimulation quickly arose. The Navy began to address these questions in 1966 with the publication of a study by the Naval Oceanographic Office on geographic and seasonal distribution (Staples, 1966), coincidentally almost simultaneously with work by the National Institute of Oceanography (Turner, 1965; 1966). This work was updated in (Lynch, 1978) and is continuing. Much research, however, is conducted outside Navy laboratories. A need existed to identify, collect, and briefly summarize relevant literature for the convenience of investigators. This bibliography updates an initial bibliography and technical assessment published in 1979-1980 (Hickman and Staples, 1979; Hickman et al., 1980).

This bibliography covers 1979 through 1987, except that Peter J. Herring's book, *Bioluminescence in Action*, published in 1978, is included because of its importance to the field and because it was omitted from the previous bibliography (Hickman and Staples, 1979). During these years much interesting work was done on bioluminescence beyond the scope of this report. This circumstance required omitting many worthwhile publications. These omissions are especially regrettable in the areas of biochemistry and genetic engineering, which, except for a few general reviews, have been included only to the extent that they could be related to possible means of manipulating light emission or to further understanding of symbiosis. With regard to bacteria, only biochemistry papers dealing with the enzymes encoded by the seven *lux* genes have been included. Papers on laboratory procedures, such as isolation and purification techniques, and characterization and identification of chemical substances, have largely

been omitted. Works on biotechnology and nonoceanographic applications have also been omitted. Without these omissions, this bibliography easily could have been half again as large as it is.

A few of the papers are incompletely referenced. These papers are abstracts supplied by their authors, without page numbers. In all cases, only the source publication and date are given. With these exceptions, the references are complete.

The citations in this bibliography are arranged alphabetically by first author, then second author, etc. Two or more papers with identical authorship are arranged chronologically, beginning with the earliest. Whenever the paper cited included an abstract or brief summary, this was used without change in this bibliography (indicated by bold uppercase letters). When such an abstract was not provided, one was written.

## Assessment

An examination of the content of the publications cited in this bibliography shows several areas of research in which there has been a major investment of effort over the last decade. Each will be briefly analyzed in relation to basic research interests in this assessment.

The greatest effort, perhaps, has gone into studying the flash characteristics of luminous marine organisms. Almost 40% of the papers cited are concerned with the measurement of flash spectra, kinetics, or intensity, or some combination thereof. New instrumentation has allowed spectral and kinetic measurements of unsurpassed accuracy and resolution to be made. These instruments are calibrated and standardized so that results from many investigators can be compared. They are easy to use, are computerized for easy data reduction and storage, and are sufficiently portable and rugged for shipboard use, so that freshly caught specimens can be examined immediately at sea. They have

been used to take spectra from large numbers of previously unmeasured luminous marine organisms, and to remeasure with greater reliability spectra of well-studied organisms. Accurate spectral and kinetic measurements are important to establish the validity of the signature concept, that is, the idea that an organism can be identified by its flash without the need for capture and taxonomic analysis. It has been shown that neither the spectrum of a flash nor its kinetics alone can distinguish reliably even among a group of very dissimilar organisms, but that together they can be used with reliability. Spectral signatures may also be able to distinguish among closely related species, but so far this has been reported (with success) only in one abstract. The work is ongoing and should be reported soon in a complete paper.

New photometers and bathyphotometers have been developed for measuring flash and glow intensities from single organisms on shipboard or from populations in situ. Standardization has not progressed as far in in situ instruments, however, as it has in instruments designed for shipboard and laboratory use. New bathyphotometers are still being built and tested to overcome problems of sampling, geometry, stimulation, and variable lag times, and to allow for rapid, high volume sampling at variable depths to increase area coverage.

Studies on techniques and mechanisms for stimulating bioluminescence make up about 15% of the papers in this bibliography. In terms of progress, however, this area lags behind flash characteristic studies. The majority of research has been done on electrical or electromagnetic stimulation, chemical stimulation (chemicals may inhibit as well as stimulate, but studies of chemical inhibition have generally been directed toward elucidating biochemical or physiological mechanisms of luminescence regulation instead of toward the inhibition itself), or mechanical stimulation using a piezoelectric crystal. These methods have been used because they can deliver an easily quantifiable, controllable, repeatable pulse or train of pulses for simple experimental design. However, other sources of stimulation likely to be encountered in the ocean—namely turbulence, acceleration, velocity, and shear fields, and sudden pressure changes—have proven difficult to address. In particular, it has been difficult to separate the individual effects of shear, acceleration, velocity, and turbulence in hydrodynamic flow fields, or to set up an experiment in which these change in a consistent, predictable, and

quantifiable way. Clearly, changes in these parameters act as stimuli, and steady-state fields do not stimulate light emission; but threshold and optimum rates of change have not been successfully established for any organism with certainty, nor is the response intensity to a given stimulus known. Furthermore, the response may depend on the past history of stimulation of the organism, i.e., whether it has been previously unstimulated (first flash), whether it is fatigued or exhausted (either the mechanoreceptors or the chemical components of the luminescence system), or whether a series of subthreshold stimuli has resulted in facilitation.

Other means of stimulation have received scant attention. Only two, vastly different experiments on photic stimulation have been performed, and neither was followed up. Photic techniques offer a possible means of stimulating bioluminescence remotely, and therefore may have application in distribution studies. Sonic stimulation is even less studied; it has been pursued almost entirely by the Soviets.

Although nearly 20% of the papers cited have dealt with the geographic, seasonal, and/or vertical distribution of bioluminescence, and/or with correlations with various environmental parameters, little real progress has been made. The bright spots are the development of new, standardized, calibrated, in situ bathyphotometers for shipboard use, as has already been discussed, and the concept of the light budget, which for the first time offers a tool for analyzing the luminescence field of the ocean in terms of the kinds of emitting organisms present and the relative amount of light they contribute. This concept has the potential of allowing estimates of luminescence intensity from a volume of water to be made, given historical records of the biota in the area. The problems are that adequate sampling for reliable statistical analyses of either short-term or long-term variations are difficult and costly.

Two reasons for this situation are the high cost of cruises and the scarcity of available ship time. These could be alleviated, but not eliminated entirely, by the development of floating bathyphotometers capable of long-term deployment in the manner of current meters, and by the use of remote-sensing techniques. A moored bathyphotometer for studying Diel vertical variations of bioluminescence was developed and tested in Scripps Canyon, but further development has not been reported. Remote sensing of bioluminescence has also been neglected, in part due to lack of a means of remote stimulation that

could allow statistical analysis of areas in which bioluminescence appeared and that could be rigorously related on a theoretical basis to in situ shipboard bathyphotometer measurements.

Studies of small-scale horizontal bioluminescence distribution, or patchiness, are in their infancy. Only a few measurements, even of the proper scale to use for the studies, are available. Studies of the other small-scale bioluminescence phenomenon, vertical layering, are much more advanced. It is now reasonably apparent that the principal environmental forcing factors for vertical bioluminescence distribution during the day are sunlight intensity and nutrient availability. Diel variations at dawn and dusk due to vertical migration of the various organisms composing the sonic scattering layers (both luminescent and nonluminescent) and release from photoinhibition of nonmigratory near-surface luminous organisms, such as certain photosynthetic dinoflagellates, are well documented and described. However, the driving parameters of the nighttime vertical structure are not so well established. A growing body of data implicates temperature gradients, such as the thermocline or thermal fronts, as an important factor in both vertical layering and patchiness; but all other suggested correlations, except the established correlation with salinity gradients near fresh-water sources, are relatively uncertain and inconsistent, or are highly scale-dependent, applicable only on a large or a small scale, but not both.

Almost 30% of the papers cited are concerned with luminous organisms themselves. These involve mostly taxonomy, morphology of light organs, and the functions of bioluminescence. Taxonomic studies have continued at a steady pace. The major breakthrough has been the clarification of the taxonomy of luminous bacteria based on genetic cluster analysis. This work has brought order to what was previously a highly confused subject. Studies on the morphology and ultrastructure of light organs have been extended to a number of previously undescribed species, with no new or startling discoveries. Some light organ structures have been examined in terms of their capacity to support and regulate symbiotic luminous bacteria. This work will be discussed below. It is now evident that there is no single function for bioluminescence in marine organisms; instead, each organism uses it in an individual manner. Indeed, some organisms have multiple uses. Multiple uses are well documented in flashlight fish and ponyfish (Anomalopidae and

Leiognathidae). Also, light emission in both the red and the blue spectral regions, from separate photophores, has been documented in several organisms, and separate functions have been suggested for each emission. Counterilluminating is now a widely accepted function for many organisms, and many studies have been performed on the regulatory capacity and mechanisms of counterilluminating organisms. An interesting modification of the counterilluminating theory, namely, disruptive illumination, in which the downward illumination from the emitting organism fails to match exactly downwelling background illumination, has been suggested for some organisms. It is further suggested that these organisms are preyed upon by predators with limited visual acuity, so that the ventral light emission can still provide protection without stringently matching the background.

Good progress has been made in studies of symbiosis, which make up about 13% of the papers cited. It is theorized that, from the standpoint of the higher organism in symbiosis with luminous bacteria, maximum benefit will be realized by maximizing bacterial light emission while minimizing bacterial growth. Several mechanisms by which this might be accomplished, including low osmolarity and limitation of nutrients, oxygen, or iron, have been demonstrated in laboratory studies on luminous bacteria; and light organ structures which may play a role in this regulation have been identified; but which of these possible mechanisms is actually used in nature has not been established for any organism. Even more exciting is the work that has been done in identifying the *lux* genes in luminous bacteria, the enzymes they encode, and the roles of those enzymes. This work provides a solid theoretical foundation for autoinduction, the role of aldehyde in the bioluminescence reaction and the mechanism by which the aldehyde is synthesized, and the biophysical nature of bacterial luciferase, and will eventually provide a basis for whatever mechanism (or mechanisms) of physiological control of bacteria in symbiosis is finally established. In addition, it has potential applications far beyond those addressed within the scope of this bibliography.

A final area of research concentration was the circadian rhythm of bioluminescence in dinoflagellates. Papers dealing with this topic make up about 12% of this bibliography. It is now well established that a single endogenous clock, cued externally by sunlight, drives all the circadian rhythms in dinoflagellates, which include spontaneous

flashing, stimulated flashing capacity, glow, luciferin and luciferase synthesis, chloroplast and luminelle deployment, and photosynthesis, among others. Many genetic and physiologic clock characteristics have been established, but the clock itself remains elusive. An interesting observation is the possibility of intercellular communication, via the medium, of some element that synchronizes clocks among originally asynchronous populations. Another interesting discovery is the great variation between the clock-controlled processes of individual dino-flagellates and those of the population as a whole.

An analysis of research trends in the six areas of interest shows a remarkable long-term constancy in the level of research effort over the study period. The graph shows the number of publications each year in each area. There is some overlap because many publications contain work relevant to two or more areas. Due to this overlap and to the fact that these areas of interest do not represent the entire body of literature included in this bibliography, no attempt was made to look at total publications for each year.

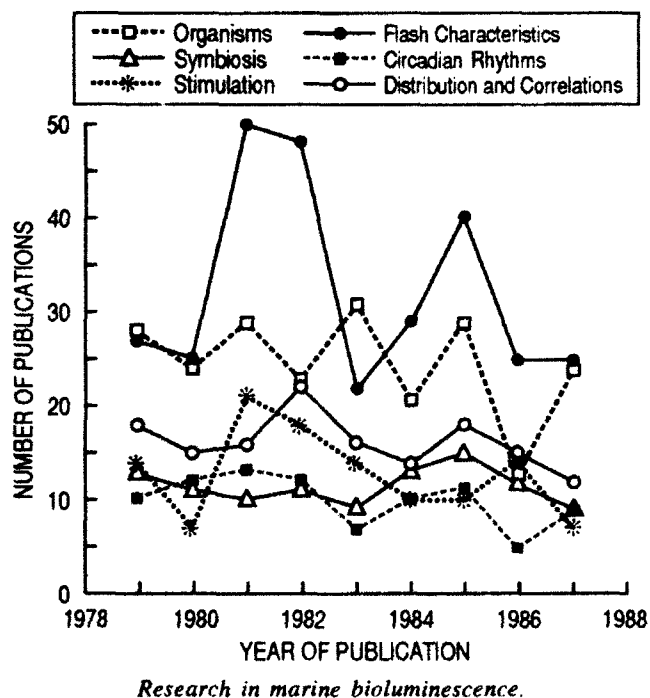
As can be seen from the graph, year-to-year fluctuations are large, a situation that leads to a large standard deviation. No point on any curve varies from the average by more than three standard deviations, and most do not exceed two standard deviations. Thus, the variations can be considered

insignificant. A closer look at two apparent features, the bulges in publications in several areas in 1981-82 and again in 1985, can partly be explained by the publication in 1981 of two major books, *Bioluminescence: Current Perspectives* and *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, and in 1982 of the book, *Bioluminescence in the Pacific*, all of which contained numerous articles included in this bibliography. If a correction is made for these one-time special publications, the 1981-82 bulge disappears. The 1985 bulge, however, cannot be explained in this manner, since no significant book was published in that year.

A look at the end points of the curves suggest a small drop in research productivity in three areas: stimulation of bioluminescence, distribution and correlations, and symbiosis. Although the number of publications in 1987 is down in all areas from 1979, and although the end-point deviations at both ends are within two standard deviations of the average, the large percentage drop in the three areas mentioned hints at a possible long-term downward trend that might manifest itself if the study period were extended.

Aside from the possibility that 1987 might simply be an off year, the methods used to find publications for inclusion in the bibliography may contribute to the appearance of a possible downward trend. The search methods were database searches by the Maury Oceanographic Library; personal scrutiny of the contents of the journals to which both on-site libraries subscribe, plus reprints sent to the author by his colleagues at other institutions; and examination of the references cited in publications received. Of these three search techniques, the library database search turned up an estimated 30% of the publications included; most of the rest were found by examination of the references cited in other works. Since time is required for an article to achieve a citation record, the heavy reliance on citations might result in a slight bias against more recent literature.

A final possibility to account for the seeming downward research trend in the three interest areas is that the trend is real, but represents the divergence of research effort into other areas of bioluminescence research, rather than a slackening of effort. Although the remaining three areas discussed in this assessment do not show a corresponding increase in publications, the six areas altogether account for only a part of the total coverage of the bibliography:



and marine bioluminescence-related research is only a part of the entire field. Based on the experience of this literature search, I estimate that 250-300 publications on bioluminescence appear each year, with marine bioluminescence accounting for only 25-30% of the entire field. The total number of publications also appears to be growing, especially in the area of biotechnology.

U.S. scientists have dominated the research effort in bioluminescence, although many countries are performing active work. Table 1 shows the numbers and percentages of publications by scientists of various nationalities. The percentages add up to more than 100% because of international collaborative efforts. Altogether, scientists from 23 nations have contributed publications that appear in this bibliography. U.S. scientists have appeared as authors or coauthors on more than 60% of the total; Soviet scientists have been responsible for slightly more than 12%.

Many institutions also have been involved in the bioluminescence research effort. In this bibliography authors were affiliated with 172 different institutions. In addition, four publications were written by freelancers and the affiliations of three authors could not be determined. Of the 172 institutions involved, 9 were commercial firms, 15 were government laboratories, and the remainder were academic institutions, including universities, museums, research institutes, laboratories, academies, and foundations. Table 2 shows the most productive institutions. In the next decade, we may expect less productivity from Scripps Institution of Oceanography, Princeton University, Annamalai University, and the Naval Research Laboratory, due to retirement, graduation, or transfer of key personnel to other institutions, but more productivity from the Marine Biological Laboratory of Woods Hole Oceanographic Institution, which has acquired two important researchers in the past several years.

Funding sources for this research have been limited and joint funding has been common. In the remainder of this paragraph, sponsorship is considered only for publications written wholly by U.S. authors or for papers with joint U.S.-foreign authorship, the U.S. portion of the paper. Within this limitation, more work was funded, in whole or in part, by the National Science Foundation (NSF) than by any other agency. NSF funding was acknowledged on 227 papers, or about 30% of the total work. The Office of Naval Research funded 128 papers, or about 17%, and the National Institute

Table 1. Nationality of authors of publications in this bibliography.

Nationality	Number of Papers	Percent of Total Publications
United States	488	63
Soviet Union	95	12
Great Britain	49	6
Canada	40	5
Germany	38	5
Japan	31	4
France	30	4
Belgium	16	2
India	15	2
Israel	14	2
Switzerland	6	<1
Australia	4	<1
Italy	4	<1
People's Democratic Republic of China	4	<1
Brazil	2	<1
Netherlands	2	<1
Finland	1	<1
Greece	1	<1
Monaco	1	<1
Poland	1	<1
South Africa	1	<1
Spain	1	<1
Sweden	1	<1

of Health funded 109, or about 14%. These three agencies dominated the funding for U.S. research on bioluminescence. Other important single funding sources were the Department of Energy, which sponsored 24 publications, and the Smithsonian Institution, which funded 10 publications. Other U.S. Navy organizations sponsored 25 publications altogether, other Department of Defense agencies sponsored 3 and other U.S. government agencies sponsored 34. Foundation funding was acknowledged on 30 papers and private funding was acknowledged on 5. Commercial firms and state governments each funded 5 publications and foreign sources funded 1. Various universities funded 89 publications; of these, 50 were funded by the University of California system. Taken as a whole, the University of California system sponsored more research on bioluminescence than any other source except the top three government agencies.

Publication of results was extremely widespread. The citations in this bibliography include 166 journals, 44 books, 25 conference proceedings, 15 theses, and 14 individual reports or series of

Table 2. Institutions whose personnel participated in 10 or more publications included in this bibliography.

Institution	Number of Publications
Harvard University	100
University of California at Santa Barbara	63
Scripps Institution of Oceanography/University of California at San Diego	62
Institutes of Physics and Biophysics, USSR Academy of Sciences, Siberian Branch, Krasnoyarsk	54
University of Georgia	34
University of Rhode Island	34
University of California at Los Angeles	30
Institute of Oceanographic Sciences, Great Britain	28
Naval Ocean Systems Center, San Diego	26
Lomonosov Moscow State University	23
McGill University, Montreal	21
University of Hawaii	17
Université Catholique de Louvaine, Belgium	16
Ithaca College, New York	16
Princeton University	16
University of Montreal	15
Kovalevsky Institute of the Biology of the South Seas and Marine Hydrobiology Laboratory of the Ukrainian Academy of Sciences, Sevastopol	15
Annamalai University, India	14
Naval Research Laboratory, Washington, D.C.	14
Johns Hopkins University	13
Laboratoire de Bioluminescence, CNRS, France	13
Marine Biological Laboratory, Woods Hole	13
Universität von Göttingen, Germany	10

reports or other sources. Table 3 shows the most fecund of these sources. Of these sources, the top 15 were responsible for 247 publications, or about 32%; the next 25 were responsible for 166, or an additional approximately 22%. Therefore, 40 of the 264 total sources were responsible for about 54% of the publications. The three most cited journals, *Photochemistry and Photobiology*, *EOS*, and *Biological Bulletin*, contain abstracts as well as complete research articles (*EOS* contains only abstracts). If the abstracts are ignored, *Microbiology* (USSR), becomes the most important journal source for complete articles.

## Addendum

After this bibliography was compiled, *Deep-Sea Biology: Developments and Perspectives*, published in 1979 by Garland STPM Press, London, was found. This book updates his earlier work, *Aspects of Deep-Sea Biology* (1954) and meets all the criteria for inclusion in this bibliography. The book discusses the taxonomic sources of bioluminescence and its functional value to the emitting organisms, especially

counterillumination, the relationship of bioluminescence to vision, red emission, light lures, sexual dimorphism, and startle displays. In addition, it covers the physiology of light production, morphology of photophores, vertical distribution of migrating luminous organisms, and, very briefly, the intensity of emission of some groups of organisms. The use of bioluminescent bait by fishermen to attract prey is mentioned. Also, Erwin J. Bulhan's article, "Airborne Sensor Detects Fish at Night," published in *Aviation Week and Space Technology* 110 (9):609-60-63, 1979, is included here. This article discusses the use of an airborne low-light-level television camera developed by Zapata Fisheries Development Corporation from research performed by the National Marine Fisheries Service to locate fish schools at night from the bioluminescence that their movement stimulates.

## References

- Hickman, G. D. and R. F. Staples (1979). *Bioluminescence , the World's Oceans: Annotated*

Table 3. Sources of at least five publications included in this bibliography. Books are italicized.

Source	Number of Publications
Photochemistry and Photobiology/Abstracts of the Annual Meeting of the American Society of Photobiology	36
EOS	36
<i>Bioluminescence in the Pacific</i>	24
Biological Bulletin	16
Microbiology (USSR)	15
<i>Bioluminescence and Chemiluminescence: Current Perspectives</i>	14
Comparative Biochemistry and Physiology	13
Journal of Biological Chemistry	13
Journal of Comparative Physiology	13
American Zoologist	12
<i>Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications</i>	12
Abstracts of the Annual Meeting of the American Society for Microbiology	11
Biochemistry (USSR)	11
Marine Biology	11
Office of Naval Research House Publications	10
Applied and Environmental Microbiology	9
Archives of Microbiology	9
Journal of Experimental Biology	9
Doklady Akademii Nauk CCCP	8
Journal of Bacteriology	8
Journal of the Marine Biological Association of the United Kingdom	8
<i>Luminescent Bacteria</i> (USSR)	8
Proceedings of the National Academy of Science of the United States	8
<i>Abstracts of the Fifteenth Pacific Science Congress</i>	7
Biochemistry	7
Bulletin of Marine Science	7
Oceanology (USSR)	7
Abstracts of the Annual Meeting of the Western Society of Naturalists	6
Biowatt News	6
Current Microbiology	6
Journal of Experimental Marine Biology and Ecology	6
Journal of Interdisciplinary Cycle Research	6
Zoological Science (Tokyo)	6
Biology of the Cell (Biologie Cellulaire)	5
Biology of the Sea (Biologiya Morya)	5
<i>Bioluminescence and Chemiluminescence: New Perspectives</i>	5
European Journal of Cell Biology	5
Plant Physiology	5
Science	5
Society of Photo-optical Instrumentation Engineers Proceedings	5

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*the Oceans*. Naval Oceanographic Office Report TR-184.

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Turner, R. J. (1965). *Notes on the Nature and Occurrence of Marine Bioluminescence Phenomena*. National Institute of Oceanography Internal Report B4.

Turner, R. J. (1966). Marine bioluminescence. *Mar. Obs.* 36:20-29.

## **Appendix A**

### **Annotated Bibliographies**

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1. Aiken, J. and Jeffrey Kelly (1984). A Solid State Sensor for Mapping and Profiling Stimulated Bioluminescence in the Marine Environment. *Continental Shelf Res.* 3(4):455-464.

This paper describes the design and development of a solid-state sensor for the in situ measurement of stimutable bioluminescence of marine organisms. It can be towed in the Undulated Oceanographic Recorder or used in vertical profiling mode from a stationary research vessel. The sensor can detect signals from  $10^9$  quanta  $\text{sec}^{-1}$ , from a single dinoflagellate flash, up to  $10^{13}$  quanta  $\text{sec}^{-1}$ , at cell densities of  $10^4$  to  $10^8 \text{ m}^{-3}$ . Measurements of bioluminescence and associated environmental conditions are presented from a variety of deployments of the sensor in the Undulating Oceanographic Recorder.

2. Anctil, Michel (1979). The Epithelial Luminescent System of *Chaetopterus variopedatus*. *Can. J. Zool.* 57(6):1290-1310.

The epithelial luminescent gland of the aliform notopods of *Chaetopterus variopedatus* was investigated by light, fluorescence, and electron microscopy. Among the cell types present, the orthochromatic cells are closely associated with the luminescent zones and, based on fluorescence microscopy, are probably the photoprotein-containing photocytes. The orthochromatic, as well as the few mucous cells of the luminescent epithelia, are exocrine goblet cells that synthesize, pack and release large amounts of secretory products through an apical pore. Biconcave cells containing peroxisome-like granules and contributing the brush border microvilli of the epithelium are suspected to participate in the light emission process. Supportive cells packed with microfilaments are closely associated with the orthochromatic and mucous cells and probably mediate the extrusion of secretory materials and the ensuing luminescence after stimulation. A few multiciliated cells are also present. A subepidermal plexus underlies the luminescent epithelium and includes a large number of peripheral nerves and neurites ensheathed by large gliointerstitial cells and processes. Direct neuroeffector cell contacts are absent except for a few close appositions between neurites and supportive cells. The structural organization of the epithelium and of the nerve plexus is discussed in relation to possible neural and cellular control mechanisms in bioluminescence.

3. Anctil, Michel (1979). Ultrastructure Correlates of Luminescence in *Porichthys Photophores*. I. Effects of Spinal Cord Stimulation and Exogenous Noradrenaline. *Rev. Can. Biol.* 38(2):67-80.

Light emission induced by electrical stimulation of the spinal cord is associated with ultrastructural alterations of the varicose nerve endings, photocyte organelles and membranes in *Porichthys photophores*. Changes in nerve profiles appear first and include alterations of the shape, number and distribution of synaptic vesicles, as well as invaginations of the axolemma and mitochondrial swellings. Photocyte vesicles become markedly coalesced and their membranes are incorporated inside vesicular pools, whereas photocyte microvilli become sharply reduced at the cell periphery. Luminescence obtained by administration of noradrenaline is accompanied by similar, but more acute changes in the ultrastructure of photocytes, whereas no marked alteration of nerve profiles is noted after this treatment. These and other observations, such as the presence of specialized synaptic contacts, are discussed in terms of neural activity and processes within the photocytes which may lead to light production.

4. Anctil, Michel (1979). Ultrastructure Correlates of Luminescence in *Porichthys Photophores*. II. Effects of Metabolic Inhibitors. *Rev. Can. Biol.* 38(2):81-96.

Prolonged bright luminescent glows in *Porichthys photophores* are elicited by administration of 2,4-dinitrophenol (DNP) and potassium cyanide (KCN). Ultrastructural alterations of varicose nerve endings precede photocyte changes during such luminescent activity. Common alterations of nerve profiles include mitochondrial disruptions, flattening and depletion of synaptic vesicles, formation of large vacuolar cisternae and invaginations in the contour of axolemma. Protracted luminescent activity in response to DNP results in depletion of photocyte vesicle material while vesicle and ER membranes accumulate and coil inside coalesced vesicle pools and photocyte microvilli disappear completely. Although similar photocyte alterations are initially observed in KCN treated luminescing photophores, the early extinction of the response to KCN is related to deleterious, irreversible effects of this chemical on photocytes. These observations, along with some pharmacological manipulations, indicate that at least DNP acts initially and primarily on neural structures, probably the

mitochondria, to induce transmitter release and consequent photocyte activity. Based on this and earlier studies, a chain of subcellular events leading to light emission of *Porichthys* photophores is proposed and discussed.

5. Anctil, Michel (1980). Aminergic Mechanisms Associated with Luminescence Control in the Coelenterate *Renilla kollikeri*. *Amer. Zool.* 20(4):851.

**ABSTRACT.** Adrenaline locally excited luminescence in the sea pansy *Renilla kollikeri*. Propranolol suppressed this response as well as responses to electrical stimulation. 6-hydroxydopamine also abolished the electrical response. Desipramine, an uptake inhibitor of adrenergic neurons, and pargyline, a monoamine oxidase inhibitor, induced luminescence at low concentrations and enhanced excitability of response. Noradrenaline, adrenaline, and N-methyl transferase activities were detected within the colony. These observations suggest that the transmitter mechanisms responsible for luminescence excitation in *Renilla* are aminergic in nature.

6. Anctil, Michel (1983). Luminescence Control in Soft Corals, Polychaete Worms and Fish: Involvement of Neurotransmitters and Modulators. *Abstr., 15th Pacific Science Cong.* 1:506.

**ABSTRACT.** In the colonial coelenterate *Renilla* bioluminescence appears to be controlled through a catecholaminergic transmission system which acts either through direct neurophotocyte junctions or local interneural transmission. In the polychaete worm *Chaetopterus* luminescent material is extruded from photocytes through the squeezing action of myoepithelial cells whose excitatory innervation is cholinergic. In addition, bioluminescence is correlated with stimulus-initiated electrical activity in the nerve cord. The fish *Porichthys* maintains both central and peripheral neural control of bioluminescence. Adrenalin and noradrenalin may act as excitatory neurotransmitters while serotonin appears to play a modulatory role.

7. Anctil, Michel (1985). Cholinergic and Monoaminergic Mechanisms Associated with Control of Bioluminescence in the Ctenophore *Mnemiopsis leidyi*. *J. Exp. Biol.* 119:225-238.

The effects of cholinergic and monoaminergic drugs and blocking agents on luminescence responses of the comb-jelly *Mnemiopsis leidyi* were investigated,

using isolated strips of meridional cells. Catecholamines elicited dose-dependent flash activity and adrenalin was the most potent. The adrenalin response was abolished by propranolol ( $0.1 \text{ mmol l}^{-1}$ ), but not phentolamine. Reserpine ( $0.1 \text{ mmol l}^{-1}$ ) suppressed the flash response to electrical stimulation without affecting the adrenalin response. Acetylcholine (ACh) elicited flash activity which was propagated along the meridional canals. Eserine ( $0.01 \text{ mmol l}^{-1}$ ) potentiated the flash response to either ACh or electrical stimulation. Tubocurarine reduced or abolished responses to either ACh or electrical stimulation. Atropine elicited intense flash activity and potentiated the response to electrical stimulation, but failed to block the ACh response. Prolonged exposure of meridional canals to serotonin (5-HT) depressed or abolished flash responses to ACh, adrenalin and electrical stimulation. The ACh flash response was abolished by propranolol but the response to adrenalin was not altered by tubocurarine. It is concluded that nicotinic, cholinergic and beta-adrenergic mechanisms are interrelated and indirectly involved in excitation of luminescence in *Mnemiopsis*.

8. Anctil, Michel, Danielle Boulay and Luc LaRivière (1982). Monoaminergic Mechanisms Associated with Control of Luminescence and Contractile Activities in the Coelenterate, *Renilla kollikeri*. *J. Exp. Zool.* 223:11-24.

The effects of monoamines and adrenergic drugs on luminescent responses and rachidial contractions were investigated in the colony of the sea pansy *Renilla kollikeri*. Of several transmitter candidates tested, only adrenaline induced localized, phasic luminescence at low concentrations. Propranolol ( $1 \text{ mM}$ ) depressed adrenaline-induced and suppressed electrically stimulated luminescence, the latter being also abolished by 6-hydroxydopamine (6-OHDA) and reserpine. Desmethylinipramine (DMI,  $20 \text{ }\mu\text{M}$ ), an uptake inhibitor of adrenergic neurons, potentiated luminescent responses to both adrenaline and electrical stimulation and induced luminescence at higher concentrations. Pargyline, a monoamine oxidase inhibitor, produced DMI-like effects. Rachidial contractions in *Renilla* are biphasic events, which are usually spontaneous and rhythmic or can be induced by electrical stimulation. Noradrenaline and adrenaline enhanced the second phase of ongoing rhythmic contractions but failed to induce contractions. Reserpine and 6-OHDA abolished electrically

stimulated luminescence, but reserpine further depressed evoked contractions while 6-OHDA failed to affect rhythmic or evoked contractions. DMI (0.5 mM) initiated rhythmic contractile activity in quiescent preparations. These observations suggest that adrenaline or an as yet unidentified catecholamine may be involved as a neurotransmitter in luminescence control. Noradrenaline and/or adrenaline act possibly as neuromodulators for rachidial contractions in the sea pansy.

9. Anctil, Michel, Simon Brûnel and Laurent Descarries (1981). Catecholamines and 5-Hydroxytryptamine in Photophores of *Porichthys notatus*. *Cell Tissue Res.* 219:557-566.

Radioenzymatic assays and light microscope radioautographic studies performed on photophores of *Porichthys notatus* demonstrated (1) significant amounts of catecholamines (dopamine, noradrenaline, adrenaline) and 5-hydroxytryptamine (serotonin) in these organs; (2) selective uptake and storage of [ $^3\text{H}$ ]noradrenaline ([ $^3\text{H}$ ]NA) by axon terminals innervating the photocytes and (3) strong accumulation of [ $^3\text{H}$ ]5-hydroxytryptamine ([ $^3\text{H}$ ]5-HT) within the photocytes. Uptake and storage of [ $^3\text{H}$ ]NA in the nerve fibers were seemingly unaffected by the addition of ten-fold molar concentrations of unlabelled serotonin. Accumulation of [ $^3\text{H}$ ]5-HT by the photocytes was dose-dependent and diminished markedly in the presence of ten-fold molar concentrations of nonradioactive noradrenaline. Neither neuronal uptake of [ $^3\text{H}$ ]5-HT or [ $^3\text{H}$ ]NA, nor photocytic accumulation of [ $^3\text{H}$ ]NA were detectable under the conditions of the present experiments. This information should provide a framework for further investigations of the regulation of photophore luminescence by the biogenic amines.

10. Anctil, Michel, Laurent Descarries and Kenneth C. Watkins (1984). Distribution of [ $^3\text{H}$ ] Noradrenalin and [ $^3\text{H}$ ] Serotonin in Photophores of *Porichthys notatus*. An Electron-Microscopic Radioautographic Analysis. *Cell Tissue Res.* 235(1):129-136.

Photophores of *Porichthys notatus* were examined by electron-microscopic radioautography following incubation in tritiated noradrenaline ([ $^3\text{H}$ ]NA) or serotonin ([ $^3\text{H}$ ]5-HT). Nerve varicosities surrounding the photocytes were found to accumulate [ $^3\text{H}$ ]NA but not [ $^3\text{H}$ ]5-HT, providing compelling evidence for the catecholaminergic nature of the monoaminergic

innervation of photophores. The photocytes themselves appeared selectively labelled with both tracers, but the intensity of labelling after [ $^3\text{H}$ ]5-HT incubation was considerably greater than after [ $^3\text{H}$ ]NA. Stereological sampling of organelle content in photocytes showed ultrastructural differences between [ $^3\text{H}$ ]NA- and [ $^3\text{H}$ ]5-HT-labelled cells, probably related to light emission induced by NA. The main changes noted after incubation with [ $^3\text{H}$ ]NA were mitochondrial swelling and disorganization, increased coalescence of photocytic vesicles and extrusion of vesicular material into the extracellular matrix. With respect to the subcellular localization of [ $^3\text{H}$ ]NA and [ $^3\text{H}$ ]5-HT within the photocytes, statistical analysis of the distribution of silver grains disclosed a preferential affinity of both labels for appositional zones between mitochondria and coalescent vesicles. Moreover, in the case of 5-HT, selective affinity was also exhibited by sites comprising vesicular membrane and adjacent cytoplasm, suggesting binding of this biogenic amine to the entire membrane of photocytic vesicles.

11. Anctil, Michel, Guy Germain and Luc LaRiviere (1984). Catecholamines in the Coelenterate *Renilla köllikeri*. Uptake and Radioautographic Localization. *Cell Tissue Res.* 238(1):69-80.

The characteristics of uptake of  $^3\text{H}$ -noradrenaline ( $^3\text{H}$ -NA) and  $^3\text{H}$ -adrenaline ( $^3\text{H}$ -A) in the tissues of the sea pansy, *Renilla köllikeri*, were studied by in vivo incubations. Lineweaver-Burk plots indicated two components of catecholamine accumulation, one representing a high-affinity uptake with an apparent  $K_m$  of  $4.91 \times 10^{-7}$  M ( $^3\text{H}$ -NA) or  $4.39 \times 10^{-7}$  M ( $^3\text{H}$ -A), and the other a low affinity process with an apparent  $K_m$  of  $5.52 \times 10^{-5}$  M ( $^3\text{H}$ -NA) or  $1.49 \times 10^{-5}$  M ( $^3\text{H}$ -A). The high-affinity uptake of both tracers was strongly inhibited at low temperature and in a calcium-free medium, thus suggesting the involvement of a carrier-mediated transport mechanism, but was largely insensitive to sodium omission and ouabain. Accumulations of  $^3\text{H}$ -NA, but not  $^3\text{H}$ -A, were highly desipramine-sensitive. Light-microscopic radioautographic studies demonstrated the presence of cells reactive to both  $^3\text{H}$ -NA and  $^3\text{H}$ -A in the ectoderm, mesoglea and endoderm. Extraneuronal accumulations of  $^3\text{H}$ -NA and  $^3\text{H}$ -A were prominent in some ectodermal cells, in amoebocytes and spicule cells. Reactive neuronal processes were tentatively identified throughout the mesoglea and over all muscle layers on the basis of

several morphological criteria. The  $^3\text{H-A}$ , but not  $^3\text{H-NA}$  label, was more intense over the presumed photocytic zone and circular muscle than elsewhere. These and other observations support a neurotransmitter role for adrenaline (and probably noradrenaline) in control of luminescence and modulation of slow rachidial contractions.

12. Anctil, Michel and Osamu Shimomura (1984). Mechanism of Photoinactivation and Re-activation in the Bioluminescence System of the Ctenophore *Mnemiopsis*. *Biochem. J.* 221:269-272.

The bioluminescence of the ctenophore *Mnemiopsis* takes place when the photoprotein mnemiopsin in the photocytes reacts with  $\text{Ca}^{2+}$ . The luminescence is inhibited in sunlight and this photoinhibition is reversible by keeping the live specimens in the dark. The extracts of mnemiopsin are similarly photoinhibited, but the photoinhibition cannot be reversed in the dark. We have found that photoinhibited mnemiopsin can be reactivated in the dark by incubation with coelenterazine and  $\text{O}_2$  only in solutions that have a pH very close to 9.0. The reactivation in vivo probably takes place in the same manner, using the coelenterazine that is supplied from its abundant storage form. Various lines of experimental evidence suggest that the photoinactivation of mnemiopsin results in the dissociation of coelenterazine and oxygen from the molecule of photoprotein; the dissociated form of the former molecule is an inactive form of coelenterazine, not free coelenterazine.

13. Anderson, James Jay (1982). The Nitrite-Oxygen Interface at the Top of the Oxygen Minimum Zone in the Eastern Tropical North Pacific. *Deep-Sea Res.* 29(10A):1193-1201.

Observations of continuous chemical profiles through the top of the oxygen minimum zone off the Pacific coast of Mexico show a secondary fluorescence peak associated with a layer of near-zero oxygen and nitrite concentrations and large curvatures in the profiles. The layer is about 4 m thick and the oxygen and nitrite fluxes into the layer are estimated to be within a factor of 2 of  $1.5 \text{ mg-at.m}^{-2} \text{ d}^{-1}$ . The fluorescence peak is probably due to microorganisms that obtain energy for growth from the oxidation of nitrite. The integrated carbon production rate required to maintain the peak is estimated at  $1 \text{ mg-at.m}^{-2} \text{ d}^{-1}$ . Nitrification is most likely the dominant process in the

layer and the nitrifying bacteria could produce the fluorescence. Alternatively, the fluorescence might be from photosynthetic bacteria that oxidize nitrite in a manner similar to the photosynthetic oxidation of sulfur compounds, or from bioluminescence.

14. Andrews, Christine C., David M. Karl, Lawrence F. Small and Scott W. Fowler (1984). Metabolic Activity and Bioluminescence of Oceanic Faecal Pellets and Sediment Trap Particles. *Nature* 307:539-541.

Bioluminescence was detected with a shipboard photometer in 70% of all samples of freshly collected zooplankton fecal pellets, particulate matter collected with sediment traps, plankton nets, or water samplers, live animals, and crustacean molts. Live animal and net plankton samples exhibited erratic, luminous flashes while sediment-trap particles and fecal pellets showed a continuous steady glow. The latter response suggests enteric luminous bacteria as the cause of the luminescence. This suggestion has been confirmed by the isolation of luminous bacteria from fecal pellets and sediment-trap particles and exhibition of bacterial light emission characteristics. The vertical profile of particulate bioluminescence showed a peak at 30 m and a constant level of emission below 400 m. However, the "biomass specific" luminescence increased below 800 m in conjunction with a layer of enhanced biological productivity and particle production just below the oxygen minimum layer. Stimulated in situ bioluminescence also increased below 700 m. The observation of luminescence in fecal pellets of bacterial origin suggests that functional importance of luminescence in marine bacteria is related to the dispersion and propagation of the species through attracting higher trophic level organisms to feed on the pellets, thereby recycling the nutrients contained therein and facilitating the propagation of the bacteria.

15. Anonymous (1979). Insight into Squid Lighting Scheme. *New Scientist* 81:672.

Luminous deep-sea squids can control their brightness through light-receptive cell groups located on the head that act as exposure meters and measure background illumination. Luciferin is found in highest concentration in digestive glands, which apparently manufacture and store it. Luciferin is also found in two species of deep-sea octopuses, not previously reported to be luminescent, but the lack of a

distribution system and photophores suggests that it is ejected to form a luminous cloud.

16. Anonymous (1979). Bioluminescence Octopus-Style. *Science News* 115(6):88.

Bioluminescence is reported for the first time from the digestive tract of two deep-sea species of octopuses. It is speculated that the function may be to eject clouds of luminous material to confuse and distract predators, a strategy similar to that of shallow-water octopuses using dark ink.

17. Anonymous (1981). Scripps Studies Bioluminescence with Underwater Station. *Sea Technology* 22(4):53-54.

A large buoy containing instruments for measuring bioluminescence has been anchored over Scripps Submarine Canyon at about 15 m below the surface. It is capable of profiling bioluminescence to 183 m in 30 min. It can also measure spectral and kinetic flash signatures around the clock and analyze and store them using an on-shore computer system.

18. Anonymous (1981). Laser Pulses Induce Bioluminescence. *Laser Focus* 17(6):44-45.

A 1-μsec pulse at 585 nm from a rhodamine 6G dye laser induces bioluminescence in the dinoflagellate *Pyrocystis lunula*. After a lag period of 15-20 msec, peak emission occurs about 50 msec later, followed by a decay lasting about 500 msec. The emission intensity increases linearly with laser pulse intensity. Multiple stimulation leads to degradation in the flash response, with no recovery of luminescence ability after 1 hour without disturbance.

19. Anonymous (1986). Characterization, Measurement and Prediction of Marine Bioluminescence. In *Recent Accomplishments Office of Naval Research Sponsored Programs*, Office of Naval Research, Washington, D.C., October, p. 3-2.

This report summarizes work accomplished at the Naval Ocean Systems Center. J. R. Losee and A. R. Zirino, principal investigators, from FY79 to FY81. An on-board photomultiplier system for measuring bioluminescence while underway and a newly designed bathyphotometer capable of reaching depths of 100 m are described. The hypothesis that bioluminescence distribution follows plankton dynamics is tentatively confirmed. The following conclusions are reached: (1) planktonic

bioluminescence is virtually ubiquitous in the oceans; (2) intensity peaks correlate with thermal gradients and (3) can be associated with organism populations; (4) individual species produce distinct optical spectral patterns; and (5) crustacean nauplii contribute significantly to the signal.

20. Aoki, M., K. Hashimoto and Haruo Watanabe (1985). Bioluminescence in the Ascidian, *Clavelina miniata*. I. Various Stimulations Evoke Light Emission from the Test Cells. *Zool. Sci. (Tokyo)* 2(6):928.

**ABSTRACT.** Bioluminescence is reported for the first time in an ascidian, *Clavelina miniata*. It is  $\text{Ca}^{2+}$  dependent, is produced extracellularly by a specific type of cell in the tunic, and appears to be endogenous rather than due to symbiotic bacteria. A localized flash lasting 1-2 seconds can be induced mechanically, while hypotonic conditions or a change in the  $\text{K}^+/\text{Na}^+$  ion ratio induces emission from the whole tunic for 15-30 minutes.

21. Aoki, T., T. Kitamura, S. Matsuno, K. Mitsui, Y. Ohashi, A. Okada, D. R. Cady, J. G. Learned, D. O'Connor, M. McMurdo, R. Mitiguy, M. Webster, C. Wilson and P. Grieder (1985). Background Light Measurements at the DUMAND Site. *Proc., 19th Int. Cosmic Ray Conf.* 8:53-56.

Ambient light intensities at the DUMAND site are measured around the one photoelectron level. Throughout the water column between 1500 m and 4700 m, much stimutable bioluminescence is observed with a ship suspended detector. The nonstimulated bioluminescence level is comparable to, or less than, the  $\text{K}^{40}$  background, when measured with a bottom-tethered detector typical of a DUMAND optical module.

22. Arrio, Bernard, A. Binet, Alain Dupaix, Bernard L'cuyer, Chantal Fresneau and Pierre Volfin (1979). Biochemical Studies of the Bioluminescence of the Polynoid Scaleworms. *Proc., Int. Symp. on Analytical Applications of Bioluminescence and Chemiluminescence*, E. Schram and P. Stanley, eds., Westlake Village (California): State Printing and Publishing, Inc., p. 618.

**ABSTRACT.** Bioluminescence in polynoid worms is confined to the dorsal scales and does not exhibit a luciferin-luciferase reaction. Partially purified photoproteins can be stimulated to emit light by

reducing agents such as  $\text{Fe}^{2+}$  or sodium dithionite. Superoxide dismutase strongly inhibits the reaction.

23. Badcock, Julian and R. A. Larcomb (1980). The Sequence of Photophore Development in *Xenodermichthys copei* (Pisces: Alepocephalidae). *J. Mar. Biol. Assoc. (UK)* 60:277-294.

*Xenodermichthys copei* is a mesopelagic inhabitant common in the eastern North Atlantic over the slope areas of the British Isles, Bay of Biscay and the northwest African coast. When adult it bears over 500 sessile structures, which, on histological evidence, have been interpreted as being photophores despite repeated failure to elicit their luminescence. The photophores have a marked pattern of distribution about the head, body and fins, and develop sequentially over the metamorphic period (ca. 9-36 mm). Here the photophores are assigned to groups and series to allow the elucidation of the sequence of photophore development. Some study of photophore structure and size is made. The results lead to the conclusion that photophores perform vital functions during the metamorphic as well as the more advanced life stages. A combination of factors, e.g., the environment in which the animal dwells, photophore structure, sequence and orientation, suggest that photophores may function primarily in a ventral counter-illuminating capacity during the growth stages. Implicit in this hypothesis is that the photophores can match the downwelling solar light in color and intensity and that the animal is orientated horizontally, particularly during suspected periods of relative inactivity; at present there is no direct evidence in support of these assumptions. It seems unlikely, however, that counter-illumination would remain the primary photophore function throughout the life of the animal and in those with a full complement of photophores bioluminescence is probably significant in other ways.

24. Baguet, Fernand (1983). Light Production and Oxygen Consumption of Isolated Photophores of the Epipelagic Fish *Porichthys*. *Abstr., 15th Pacific Science Cong.* 1:11.

**ABSTRACT.** Oxygen consumption in isolated luminescing photophores from the fish *Porichthys* is increased over non-luminescing photophores by 1-3 nanomoles/photophore/minute for stimulating KCN concentrations of  $10^{-5}$ - $10^{-3}$  M and 0.8 nanomoles/photophore/minute for  $10^{-4}$  M adrenaline and

noradrenaline. It is suggested that this excess oxygen consumed corresponds to the oxygen involved in the light reaction and that the amount involved may depend on the nature of the controlling mechanism.

25. Baguet, Fernand (1985). Aspects Comparatifs de la Bioluminescence des Poissons Lumineux du D'troit de Messine. *Ann. Soc. R. Zool. Belg.* 115(1):61-73 (French).

Isolated ventral photophores of *Argyrolepiscus hemigymnus* and abdominal photophores of *Maurolicus muelleri* respond to adrenaline  $10^{-4}$  M by a light emission which magnitude is proportional to the weight of photophores. The amplitude of the light response is four times as high in *Maurolicus* with regard to *Argyrolepiscus* photophores. According to the counter-lighting hypothesis, this difference suggests that those fishes might live in waters of a different ambient light level.

26. Baguet, Fernand and B. Christophe (1983). Adrenergic Stimulation of Isolated Photophores of *Maurolicus muelleri*. *Comp. Biochem. Physiol.* 75C(1):79-84.

Abdominal and caudal photophores isolated from freshly captured specimens of *Maurolicus muelleri*, in the Strait of Messina, respond to adrenaline and noradrenaline by a light emission which is proportional to the fresh weight of the photophores. The maximal light emission occurs at  $10^{-3}$  M for adrenaline and is estimated at  $155.3 \times 10^6$  quanta/sec/mg; for noradrenaline it occurs at  $10^{-4}$  M and is estimated at  $45.6 \times 10^6$  quanta/sec/mg. Noradrenaline  $10^{-3}$  M largely inhibits the photophore luminescence. The photophores show the same sensitivity to isoproterenol and adrenaline on one hand and to phenylephrine and noradrenaline on the other hand. Phentolamine  $10^{-4}$  M depressed the light response to noradrenaline  $10^{-4}$  M by 80%; propranolol  $10^{-4}$  M depressed the response to adrenaline  $10^{-4}$  M by about 50%.

27. Baguet, Fernand and Jacques Piccard (1981). The Counterlighting Hypothesis: In Situ Observation on *Argyrolepiscus hemigymnus*. In *Bioluminescence and Chemiluminescence, Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 517-523.

Downwelling light intensity at three wavelengths (430, 470, and 500 nm), the vertical distribution of luminous fish, and light emission intensity at 470 nm from *Argyropelicus hemigymnus* were measured on 21 dives on the mesoscap *Forel* in the Strait of Messina at different times of day from the surface to 550 m. Qualitative observations of luminescence in myctophids, *Cyclothone braueri*, and *Argyropelicus* were also made. Fish depth distribution correlated with ambient light intensity and time of day. How strictly the fish followed a preferred isolume differed for each species. *Argyropelicus* and myctophids exhibited sustained ventral bioluminescence, but the emission intensity did not match the ambient intensity, nor did the maximal intensity of luminescence of *Argyropelicus* determined in the laboratory equal the ambient intensity encountered at sea; *Cyclothone* was nonluminous. These results do not support the counterlighting hypothesis as it is conventionally presented.

28. Baguet, Fernand, Jacques Piccard, B. Christophe and G. Marechal (1983). Bioluminescence and Luminescent Fish in the Strait of Messina from the Mesoscap "Forel." *Mar. Biol.* 74:221-229.

Light irradiance was measured at 430, 470 and 500 nm aboard the mesoscap *Forel* in the Strait of Messina from the surface to 500 m depth in May 1979. The underwater light regime is partly due to the downwelling residual sunlight and partly to bioluminescence. An intense bioluminescence is localized at about 450 m at midday and moves upwards in the evening to reach an area extending from 100 m depth to the surface late in the evening. Two types of luminescence were observed: one associated with luminescent organisms and another diffuse, probably due to bacteria. Three types of luminescent fish were recognized, namely *Argyropelecus hemigymnus*, myctophids and *Cyclothone braueri* and their time and space distribution were studied. While myctophids were encountered from the surface (21:00 hours) to 550 m depth (16:00 hours), *A. hemigymnus* were only observed between 180 m (19:45 hours) and 500 m (12:15 hours) and *C. braueri* between 330 m (16:00 hours) and 500 m (19:00 hours). The results do not show a significant relation between the absolute ambient light intensity and the time or the depth where the fish were observed.

29. Baguet, Fernand and J. F. Rees (1987). Glycolysis as a Control Mechanism of Luminescence in *Porichthys*. *Photochem. Photobiol.* 45(S):95S.

**ABSTRACT.**  $10^{-5}$  to  $10^{-2}$  M glucose or mannose inhibits bioluminescence in isolated *Porichthys* photophores without impairing the response to adrenaline or noradrenaline. These effects are observed in the presence of pyruvate but are blocked by moniodoacetate, which induces luminescence in the presence of glucose but not pyruvate. Glucose further inhibits KCN-stimulated luminescence. From this evidence it is suggested that glycolysis inhibits luminescence in non-stimulated photophores and that adrenergic neuromediators trigger a light response by inhibition of glycolysis.

30. Baguet, Fernand and A. M. Zeitz-Nicolas (1979). Fluorescence and Luminescence of Isolated Photophores of *Porichthys*. *J. Exp. Biol.* 78:47-57.

Isolated photophores of *Porichthys* exposed to ultraviolet light (365 nm) exhibit a green fluorescence localized in the photocytes and a bluish fluorescence originating from the lens-like body. The luminescence of photophores evoked by epinephrine, norepinephrine or potassium cyanide decreases with the intensity of the green fluorescence of the photogenic tissue; the bluish fluorescence of the lens-like body does not change significantly. The total amount of light emitted is a linear function of the decrease of the greenish fluorescence intensity. The slope of the regression line is maximal in response to epinephrine or norepinephrine  $5 \times 10^{-4}$  M and potassium cyanide  $10^{-3}$  M. It decreases significantly for higher concentrations. The decrease of fluorescence observed during the light emission is tentatively explained by oxidation of a luciferin present in a fluorescent form in a fresh photophore.

31. Baldwin, Thomas O. and Miriam Z. Nicoli (1979). Structural Features and the Reaction Mechanism of Bacterial Luciferase. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 151-152.

**ABSTRACT.** The reaction pathway of the bacterial light-producing reaction is shown. Physical and chemical characteristics of the two subunits of the bacterial luciferase molecule and its active site are given.

32. Baldwin, Thomas O., Tineke Berends and Mary L. Treat (1984). Cloning of the Bacterial Luciferase

and Use of the Clone to Study the Enzyme and Reaction In Vivo. In *Analytical Applications of Bioluminescence and Chemiluminescence*, Larry J. Kricka, Philip E. Stanley, G. H. G. Thorpe and T. P. Whitehead, eds., New York: Academic Press, pp. 101-104.

Bioluminescence from *Escherichia coli* containing cloned *Vibrio harveyi* luciferase genes was compared with bioluminescence from wild *V. harveyi* strains. It was found that *V. harveyi* luminescence does not require an energy transfer system and that proper folding of the  $\alpha$  subunit into a stable conformation requires the presence of the  $\beta$  subunit.

33. Ballek, Robert W. and Elijah Swift (1986). Nutrient- and Light-Mediated Buoyancy Control of the Oceanic Non-motile Dinoflagellate *Pyrocystis noctiluca* Murray ex Haeckel (1890). *J. Exp. Mar. Biol. Ecol.* 101:175-192.

It appears that nutrient concentrations rather than light intensity are the primary factors controlling the buoyancy of *Pyrocystis noctiluca* Murray ex Haeckel (1890) cells in the sea and that changes in the buoyancy of *P. noctiluca* tend to concentrate it at subsurface depths. In the southern Sargasso Sea and the northern Caribbean Sea, vegetative cells of *P. noctiluca* had population maxima at depths between 60 and 100 m at the 15 to 2% isolumens and about 0 to 70 m above the apparent depth of the nutricline. From the mixed layer to the depth of the vegetative cell population maximum, there was an increasing proportion of positively buoyant cells of *P. noctiluca*. The highest proportions of positively buoyant cells occurred from just below the depth of the vegetative cell maximum to about 170 m depth. These results suggest that cells either above or below the depth of the vegetative cell maximum tend to use their buoyancy to return to that depth. Experiments to test what affected the cell buoyancy were carried out in chambers containing *P. noctiluca* and suspended below drifting buoys in the Sargasso Sea and the Caribbean Sea. In chambers with plankton netting for sides (having ambient nutrients), *P. noctiluca* populations became negatively buoyant when held in the mixed layer 5 days, but became positively buoyant when held in the thermocline at 110 m for 5 days. In chambers having solid sides, *P. noctiluca* also became negatively buoyant in the mixed layer and at 110 m unless nutrients (including  $8.8\mu\text{M NO}_3^-$  and  $0.36\text{ M}$

$\text{PO}_4^{3-}$ ), were added to the seawater in the chambers. In the laboratory, nutrients rather than light intensity also appeared to be the primary factor controlling the buoyancy of *P. noctiluca* cells. In the laboratory, an increase in the proportions of sinking cells took place only after nutrient depletion. In cultures, light at saturating and subsaturating intensities for cell division rate apparently affected buoyancy by controlling the rates at which the cells used nutrients through growth processes. In both the sea and in cultures, cell buoyancy characteristics were apparently due to the balance of rates of nutrient accumulation due to uptake and loss due to growth.

34. Balzer, Ivonne (1981). Effekte Potentiell Membranaktiver Pharmaka auf Circadiane Rhythmik und Biolumineszenz von *Gonyaulax polyedra* (Dinoflagellate). Thesis, Universität Göttingen, Federal Republic of Germany (German).

This thesis was not available for review.

35. Balzer, Ivonne and Rüdiger Hardeland (1981). Advance Shifts of the Bioluminescence Rhythm in *Gonyaulax polyedra* by Pharmaka Potentially Acting on Membranes. *J. Interdiscipl. Cycle Res.* 12(1):29-34.

Various substances potentially acting on membranes were tested for their capability of phase shifting the free-running bioluminescence rhythm in *Gonyaulax polyedra*. Quinidine, propranolol, 1-aminoadamantane, and to a certain extent also tetracaine showed similar tendencies in their effects: suppression of bioluminescence and, hence, suppression of apparent rhythmicity at high concentrations, phase advance shifts together with gradual reduction of bioluminescence at lower concentrations. After pulses with  $5 \times 10^{-5}\text{ M}$  quinidine, the rhythm was still apparent for several periods, although absolute bioluminescence values were reduced. Variation of the phase of pulse treatment resulted in a phase response curve.

36. Baranova, N. A., G. S. Eremina, V. S. Danilov and N. S. Egorov (1982). Nature of Aldehyde-Binding Site of Different Species of Luminescent Bacteria. *Dokl. Akad. Nauk SSSR* 262(4): 1001-1004 (Russian); 69-71 (English).

Cytochrome P-450 is found in *Photobacterium fischeri* strain MJ-1, *Beneckea harveyi* strain MAV and *Photobacterium phosphoreum* at the end of the

logarithmic growth phase. It competitively binds decanal, a substrate of bacterial luciferase, a mixed-function oxygenase, and camphor. It does not compete with aldehyde binding to luciferase. Binding constants for decanal among all three species are equal. These observations suggest cytochrome P-450 rather than the 4a-peroxyflavin site on the  $\alpha$ -subunit of bacterial luciferase as the binding site of the aldehyde.

37. Baranova, N. A., A. D. Ismailov, N. S. Egorov and V. S. Danilov (1980). Cytochromes of the Luminescent Bacterium *Photobacterium fischeri*, Their Solubilization and Relation to Luminescence. *Microbiology (USSR)* 49(4):477-482 (Russian); 417-421 (English).

The hemoprotein composition of the luminescent bacterium *Photobacterium fischeri* and the characteristics of the distribution of the cytochrome among the bacterial fractions were studied: the cell free extract, the supernatant, the "particles," and the protein preparation. It was shown by hemochromogenic analysis that the main hemoproteins of *P. fischeri* are cytochromes with heme of the b and c types. The luciferase activity is distributed together with hemoproteins. The purified luciferase preparation contains a cytochrome of the  $\beta$  type that has been identified as a mixed function oxidase, P-450.

38. Bartsev, S. I. (1982). On Possible Mechanisms of Autooscillations in Bioluminescent System of Bacteria. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 349-361.

A model is proposed to account for the discrepancy between oscillations in luminescent emission from small populations of bacteria and the lack of oscillations from single cells. It is proposed to test this model by looking for a hysteresis effect in luminous intensity with changes in intracellular  $\text{NADH}_2$  concentration.

39. Bartsev, S. I. (1984). Timing of Bacterial Luminescence. In *Luminescent Bacteria* (English translation of *Svetyashchiyesya Bakterii*, Ye. N. Kondrat'yeva, ed., Moscow: Izdatel'stvo Nauka), pp. 148-155. JPRS-UBB-85-018-L, 31 October 1985.

See Rodicheva, E. K. (1984) in this bibliography. This work constitutes the last section of that chapter.

40. Bartsev, S. I. and I. I. Gitel'zon (1985). The Question of Temporal Organization of Bacterial Luminescence. *Stud. Biophys.* 105(3):149-156 (Russian).

The conditions causing pulses in light output of a single luminous bacterium were studied. Theoretical analysis and experimental data showed the possibility that light impulses arise to increase essentially under substrate limitation of the energy metabolism and in the late stationary phase.

41. Basch, Lawrence V. (1983). Feeding Ecology and the Role of Bioluminescence in Predation in the Subtidal Sand-Dwelling Brittle-Star *Ophiopsila californica*. *Amer. Zool.* 24(4):1018.

**ABSTRACT.** Bioluminescence functions in prey capture by *Ophiopsila californica* by stunning and thereby subduing motile, photoreceptive zooplankton when they physically contact it.

42. Basch, Lawrence V. (1985). Ecology, Behavior, and Functions of Bioluminescence in the Subtidal Sand-Dwelling Brittle-Star *Ophiopsila californica* (Echinodermata: Ophiuroidea: Ophiocomidae). MA Thesis, University of California, Los Angeles.

*Ophiopsila californica*, found along the California coast and Channel Islands, emits light upon contact by prey to stun and subdue photoreceptive zooplankton. A variety of luminescent displays along with other behavior also acts to deter predation by altering the behavior and movements of visual crustacean and fish predators into avoidance patterns.

43. Bassot, Jean-Marie (1979). Sites Actifs et Facilitation dans Trois Systemes Bioluminescents. *Arch. Zool. Exp. Gen.* 120:5-24 (French).

In three bioluminescent systems, the elytra of scale worms, the syllid *Pionosyllis* and the siphonophore *Hippopodius*, the facilitation of successive flashes is analyzed with photometrical records, in correlation with autophotographic pictures taken through a microscope and image intensifier. Facilitation is always related to recruitment of new units of activity.

44. Bassot, Jean-Marie (1987). A Transient Intracellular Coupling Explains the Facilitation of Responses in the Bioluminescent System of Scale Worms. *J. Cell Biol.* 105:2235-2243.

Isolated elytra of polynoid worms emit a flash of bioluminescence when stimulated by an electric shock. With repeated stimulation, hundreds of flashes can be elicited which, in typical series, exhibit large and progressive variations. The amount of luminescence emitted by each flash first increases during a period of facilitation and then decreases exponentially during a longer period of decay. Through a microscope and image intensifier, the activity of individual microsources or photosomes was observed, using their fluorescence as a natural probe, in that its intensity is a function of the amount of luminescence previously emitted. Sequential observation showed a progressive and basically intracellular recruitment that correlated with facilitation. Facilitation and/or recruitment depended on the frequency of the stimulation. Recruitment proceeded among the photosomes of each photocyte, beginning with those of the cell periphery and progressing to those of the center. When the repetitive stimulation was interrupted and then resumed, the refacilitation was a function of the duration of the pause, and the pathway of recruitment duplicated that of the preceding sequence. It therefore appears that, within a given cell, individual photosomes can be either coupled and respond to stimulation or uncoupled and quiescent, that the coupled state has a basic lifetime of about 1 sec which can be lengthened by reinforcement, and that this state must be established in a matter of milliseconds as a result of the stimulation. In preparing an increased response to a forthcoming stimulation, coupling acts as a short-term memory.

45. Bassot, Jean-Marie and Marie-Thérèse Nicolas (1982). A Membrane Photoprotein in Paracrystals of Endoplasmic Reticulum. *Biol. Cell.* 45(2):238.

**ABSTRACT.** The intracellular sources of bioluminescence in polynoid scaleworms are paracrystals (20-30 per cell) called photosomes, made of 200 Å tubules of endoplasmic reticulum curved and linked following a repetitive mesh. The flash is due to a photoprotein and is triggered by a  $\text{Ca}^{2+}$ -controlled action potential. It may be stimulated electrically or by superoxide radical-generating chemicals such as Fenton reagent. Peak light emission is at 510 nm.

46. Batchelder, Harold P., Jeffrey van Keuren and Elijah Swift (1987). Planktonic Bioluminescence Distribution and Intensity in the Northwestern Atlantic during May and August 1987. *EOS* (50):1707.

**ABSTRACT.** In May and August 1987 depth profiles of bioluminescence were obtained from the Sargasso Sea and near the North Wall of the Gulf Stream. Bioluminescence was higher in the Sargasso Sea in May than in August and (in May) twice as high as near the Gulf Stream North Wall. Bioluminescence intensity and vertical profiles of bioluminescence both were more variable near the North Wall. In the Sargasso Sea the bioluminescence peak was usually below the surface mixed layer and sometimes, but not always, coincided with the fluorescence peak. Low intensity flashes attributable to dinoflagellates were present near the North Wall but not in the Sargasso Sea.

47. Batchelder, Harold P. and Elijah Swift (1986). Near-surface Planktonic Bioluminescence during Summer 1986 in the Western North Atlantic. *EOS*(44):970.

**ABSTRACT.** Total bioluminescent capacity in the Sargasso Sea in July 1986 was greater than  $1 \times 10^{14}$  photons per  $50 \text{ m}^3$ , while it was  $1.5 \times 10^{13}$  photons per  $50 \text{ m}^3$  north of the Gulf Stream. The major light producers south of  $39^\circ\text{N}$  were dinoflagellates of the genus *Pyrocystis*, but these were not found north of  $42^\circ\text{N}$ . Larvaceans and ostracods also contributed importantly to the light field in the Sargasso Sea, but not north of the Gulf Stream. The light contribution of copepods and euphausiids was relatively constant with latitude; but individual contributing species within the groups changed, with *Pleuromamma* and *Lucicutia* sp. contributing in the south while *Metridia lucens* was important in the north.

48. Baumann, Paul and Linda Baumann (1981). The Marine Gram-Negative Eubacteria: *Genera Photobacterium, Beneckea, Alteromonas, Pseudomonas, and Alcaligenes*. In *The Prokaryotes: A Handbook on Habitats, Isolation, and Identification of Bacteria*, Mortimer P. Starr, Heinz Stolp, Hans G. Trüper, Albert Ballows and Hans G. Schlegel, eds., New York: Springer-Verlag, pp. 1302-1331.

The marine gram-negative eubacteria are divided into six genera and the physical, morphological, physiological, biochemical, and genetic characteristics defining each genus are described and tabulated. The species and groups within each genus are identified. Nutritional requirements for both survival and growth are specified. Unusual properties, habitats and geographic distribution are also tabulated for the

named species. Methods of isolation, preservation, and identification are given.

49. Baumann, Paul, Linda Baumann, Sookie S. Bang and Marilyn J. Woolkalis (1980). Reevaluation of the Taxonomy of *Vibrio*, *Beneckeia* and *Photobacterium*: Abolition of the Genus *Beneckeia*. *Curr. Microbiol.* 4:127-132.

**ABSTRACT.** As a result of studies on the evolution of glutamine synthetase and superoxide dismutase, the genus *Beneckeia* has been abolished and its constituent species, along with *Photobacterium fischeri* and *P. logei*, assigned to the genus *Vibrio*. The definitions of *Vibrio* and *Photobacterium* have been modified accordingly.

50. Baumann, Paul, Linda Baumann, Marilyn J. Woolkalis and Sookie S. Bang (1983). Evolutionary Relationships in *Vibrio* and *Photobacterium*: A Basis for a Natural Classification. *Ann. Rev. Microbiol.* 37:369-398.

Genotypic analyses, consisting of in vitro DNA/DNA and r-RNA/DNA hybridization and microcomplement fixation of three enzymes, GS, SOD and AP, and phenotypic analyses, consisting of modulation of the activity of the enzyme aspartokinase and nutritional screening, are compared for effectiveness in establishing a logically consistent and theoretically sound taxonomic classification among strains of *Vibrio* and *Photobacterium*, based on evolutionary relationships. It is found that no single test is sufficient to establish a standard classification procedure, but that correlation coefficients between sequence changes of r-RNA, GS, SOD and AP can be used to establish vertical evolutionary relationships among bacterial strains. Although inconsistencies arise when single factors are compared, especially on group fringes, probably from horizontal genetic exchange, sufficient sequences are conserved in the group of indicators as a whole to establish valid classification procedures. A theory for the relatively low frequency of genetic exchange is discussed.

51. Biggley, William H., Theodore A. Napora and Elijah Swift (1981). The Color of Bioluminescent Secretions from Decapod Prawns in the Genera *Oplophorus* and *Systellaspis* (Caridea). In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis (Minnesota): Burgess Publishing Co., pp. 66-81.

The spectra of four prawns in two genera were measured and found to be identical, with peak emission at 457 nm. A comparison with spectra reported from other prawns suggests identity throughout the Caridea.

52. Bityukov, E. P. (1982). Seasonal Variability and Spatial Non-Uniformity of Bioluminescence in the Mediterranean Sea. *Ekol. Morya* 8:10-20.

Bioluminescence measurements have been made at 152 stations in the Mediterranean Sea over a 12-year period. The vertical structure of the emission field suggests alternating layers, 3-7 m in thickness and relatively stable in depth. Seasonal variations occur and a general increase in bioluminescence is noted going from east to west. In most regions layers of increased bioluminescence are observed in the thermocline and from 60 to 130 m, corresponding to the core of subsurface Atlantic water of reduced salinity; layers of decreased bioluminescence are seen near the surface and from 15-30 m below the thermocline. In the Sardinian Sea well-defined layers are not found in winter and spring, but are present in summer. Layers with mean intensities of about 12, 22 and  $42 \times 10^{-5} \mu\text{W}/\text{cm}^2$  are identified. Between layers mean intensity is about  $2 \times 10^{-5} \mu\text{W}/\text{cm}^2$ . In the Ionian Sea, measured intensities range from about 2.5 to  $9 \times 10^{-5} \mu\text{W}/\text{cm}^2$ . Intensity levels increase toward the center of these seas and in summer and decrease near Malta and Sicily. Intensities of about  $1 \times 10^{-5} \mu\text{W}/\text{cm}^2$  in the Aegean Sea and 29 to  $55 \times 10^{-5} \mu\text{W}/\text{cm}^2$  in the Alboran Sea and near Gibraltar in summer are reported; in spring, intensities in the Alboran Sea can reach 135 to  $260 \times 10^{-5} \mu\text{W}/\text{cm}^2$ . In the Balearic Sea in summer, the intensity level is about  $2 \times 10^{-5} \mu\text{W}/\text{cm}^2$ , while in the Ligurian Sea it ranges from 0.2 to  $0.5 \times 10^{-5} \mu\text{W}/\text{cm}^2$ . In the Tyrrhenian Sea an intensity of about  $8 \times 10^{-5} \mu\text{W}/\text{cm}^2$  is reported, varying by a factor of 8, depending on location, with an increase toward the southeast. Spatial variations are highly dependent on water and wind dynamics.

53. Bityukov, E. P. (1984). Horizontal Heterogeneity of the Bioluminescent Field as an Index of Aggregated Plankton Distribution. *Gidrobiol. Zh.* 20(5):24-31 (Russian).

The two-dimensional picture of micro-heterogeneity of the bioluminescent field is obtained from bioluminescent profiles in 50 m on the 2.7-km transect down to the 100-m depth using the procedure

of the plankton space structure visualization by bathyphotometric sounding. Horizontal various-scale heterogeneities are detected in the horizons and layers. Minimal heterogeneities corresponded to the same profile of measurements. Maximal length of the heterogeneity differing in the intensity more than thrice extended up to 350 m. In the upper 50-m thickness 22 to 27 heterogeneities are observed. The phase relations between bioluminescence distribution and the temperature field are unstable and characterized by the absence of horizontal coherence.

54. Bityukov, E. P. and V. I. Vasilenko (1979). The Bioluminescent Field of the Pelagic Zone of the Southern Atlantic. *Biol. Morya* (Kiev) 49:37-42 (Russian).

The spatial distribution of bioluminescence in the pelagic zone of the South Atlantic was measured to 200 m by continuous bathyphotometric sounding. Alternating layers and correlations with the thermocline and frontal regions were observed. The brightest bioluminescence was found in equatorial waters, the Brazil Current, and upwelling regions near Brazil and the Falkland Islands. Intensity values for many areas are reported.

55. Blizard, Marvin A., Eric O. Hartwig and Bernard J. Zahuranec (1982). Marine Bioluminescence and Optical Variability. Report on the Office of Naval Research Advisory Group Meeting, 5-6 December 1982, Berkeley, California.

The report documents the recommendations of the ONR-sponsored Advisory Group Meeting on Marine Bioluminescence and Optical Variability held in Berkeley, California on 5-6 December 1982. The Oceanic Biology and Underwater Optics Programs (Code 422CB and 4250A) of the Office of Naval Research are planning for a 5-year initiative (Special Focus Program) in this area beginning in October 1983. This report represents an input of primarily the academic community to the planning of this initiative.

56. Boalch, G. T. (1979). The Dinoflagellate Bloom on the Coast of South West England, August-September 1978. *J. Mar. Biol. Assoc. UK* 59(2):515-517.

During the last week of August and the first two weeks of September, 1978, red tides and fish kills were reported along the south coast of Cornwall.

Large numbers of the luminous dinoflagellate *Noctiluca scintillans* were associated with the phenomenon.

57. Bochkova, G. B., S. V. Ermolin and B. S. Rodichev (1985). The Influence of Superhigh Frequency Electromagnetic Fields on the Bioluminescence of *Vibrio harveyi*. *Radiobiologiya* 25(3):362-366 (Russian).

Exposure of bacteria *V. harveyi* grown on agar medium to 7 HHZ electromagnetic field changes the intensity of their luminescence. It is suggested that the dynamics of the luminescence change reflects the adaptation processes in the microorganisms which accompany the electromagnetic field effect. The changes observed may be attributed to the temperature dependence of bioluminescence.

58. Boksha, I. S., V. S. Danilov, and N. S. Egorov (1985). Interaction of Ferricytochrome c with Bacterial Luciferase. *Biochemistry* (USSR) 50(1):122-127 (Russian) :110-115 (English).

The mechanism of the inhibition of the bacterial luminescent system from *Beneckea harveyi* by ferricytochrome c was investigated. It was shown that inhibition is associated with the presence of NADH:cytochrome c reductase activity. The direct action of cytochrome c on bacterial luciferase was investigated, and the presence of a shunt of electron transport at the level of the structural component of luciferase-lumiredoxin was suggested.

59. Bovlan, Michael, Angus F. Graham and Edward A. Meighen (1985). Functional Identification of the Fatty Acid Reductase Components Encoded in the Luminescence Operon of *Vibrio fischeri*. *J. Bacteriol.* 163(3):1186-1190.

A clone of DNA, obtained from the luminescent bacterium *Vibrio fischeri* ATCC 7744 and inserted in pBR322, was found to express luminescence in *Escherichia coli*. Polypeptides involved in biosynthesis of the fatty aldehyde substrate for the light reaction were identified by fatty acid acylation of proteins synthesized in *E. coli* from the recombinant plasmid. The cloned region was similar to that reported for the *V. fischeri* MJ1 luminescence system except for some differences in endonuclease restriction sites and the requirement of a lower temperature for the expression of light in our cloned system. Fatty acid reductase activity could be detected in extracts of *E. coli* harboring the recombinant plasmid but not in extracts

of the parental *V. fischeri* strain. Using in vivo labeling with [<sup>3</sup>H]tetradecanoic acid, we showed that the acylated polypeptides synthesized in the cloned system corresponded to the labeled polypeptides in *V. fischeri* (34, 42 and 54 kilodaltons) and that they could only be detected after induction of luminescence. These results provide direct evidence that the genes coding for the fatty acid reductase polypeptides are an integral part of the luminescence operon in the *V. fischeri* luminescence system.

60. Bozin, S. A. and V. S. Filimonov (1985). Spontaneous Bioluminescence of Dinoflagellates in Vostok Bay, Sea of Japan. *Oceanology (USSR)* 25(3):395-397 (English).

The results of a 5-day parallel measurement of spontaneous bioluminescence in dinoflagellates, their number and the numbers of zooplankton in plankton samples are presented. It is suggested that spontaneous bioluminescence in dinoflagellates may be regarded as mechanically simulated at a stimulus intensity close to the threshold value. The stimulus is collision of dinoflagellates with zooplankton and also probably with the walls of the container in which they are kept during measurement of spontaneous luminescence. It is demonstrated that the spontaneous bioluminescence of dinoflagellates is a good indicator of their numbers (correlation coefficient for 5 days' measurements, 0.90) and is not subject to diurnal variations.

61. Bradner, Hugh, M. Bartlett, Grant Blackinton, J. Clem, David M. Karl, J. G. Learned, Alan J. Lewitus, S. Matsuno, D. O'Connor, W. Peatman, M. Reichle, C. Roos, J. Waters, M. Webster and Mark A. Yarbrough (1987). Bioluminescence Profile in the Deep Pacific Ocean. *Deep-Sea Res.* 34(11):1831-1840.

The vertical profile of bioluminescence at a station near Hawaii has been measured to a depth of 4300 m using a calibrated instrument with a threshold sensitivity of 400 photons cm<sup>-2</sup> s<sup>-2</sup>. The measured light is dominated by flashes over a very faint ambient background. The median light levels follow an exponential scaling law below 2000 m and decrease at the rate of 1/e per kilometer. Stimulated bioluminescence is observed in the wake of the instrument, even at depth.

62. Brehm, Paul and Kathleen Dunlap (1984). Control of Light Emission from *Obelia* Photocytes. *Biol. Bull.* 167:523-524.

**ABSTRACT.** In photocytes of *Obelia geniculata* step depolarizations to potentials above 0 mV from holding potentials below -30 mV evoked outward currents which reached their peak within a few ms and inactivated fully during 200 ms pulses. No voltage-dependent inward currents were observed. In small clumps of cells containing a single photocyte depolarization of a nonphotocyte elicited light flashes in the neighboring photocyte. Also, at potentials eliciting light emission from the photocyte, voltage-dependent inward currents were observed in the nonphotocyte. These results suggest that non-photocytes are required for light production from photocytes by acting as inward current generators. Stimulation experiments using isotonic KCl produced similar results.

63. Brehm, Paul, K. Takeda and Kathleen Dunlap (1985). Control of Light Emission from Cells Containing Endogenous Ca-Activated Photoprotein: Roles of Ca Current and Gap Junctions. *Biol. Bull.* 169:548.

**ABSTRACT.** Photocytes of the hydrozoan coelenterate, *Obelia geniculata*, which contain a Ca-activated photoprotein, do not emit light following direct electrical stimulation or high K application. However, luminescence is stimulated by these methods if the photocyte is associated with at least one non-photocyte support cell (and the electrical stimulation is applied to the support cell). Removal of Ca from or addition of Cd to the external medium blocks light emission. Photocytes exhibit only an outward K current, while support cells show both an inward Ca current and an outward K current. Reduction of the inward Ca current reduces bioluminescence and gap junction uncouplers reversibly block luminescence in response to depolarization of the non-photocytes. These findings suggest that the non-photocyte Ca current may trigger the passage of a Ca-dependent signal through gap junctions and that it is the critical trigger in control of luminescence.

64. Brinton, Edward (1987). A New Abyssal Euphausiid, *Thysanopoda minyops*, with Comparisons of Eye Size, Photophores, and Associated Structures

among Deep-living Species. *J. Crustacean Biol.* 7(4):636-666.

*Thysanopoda minyops*, found from 3600- to 5000-m depth in the central north Pacific, is a large (>120 mm) euphausiid. This species has small eyes with few facets but with large crystalline cones. Photophores seem to be lacking, but where the first abdominal photophore is usually present on euphausiids, there is a specialized, ventrally protruding process (lobe) of unknown function. Bathypelagic (1000 to 3,000 m) *Thysanopoda cornuta* and *T. spinicaudata* possess similar first segment lobes but also have such lobes on the fifth segment. Occurrence of similar lobes in relation to photophores in the several mesopelagic euphausiids, especially the vertical migrators, is described. Epipelagic species possess photophores but lack the lobes. Apparently blind, deep-living *Bentheuphausia amblyops* lacks photophores but has a series of lobes like those in the above species. Unique eye-size changes in relation to body length in deep-living *T. cornuta* and *T. egregia* are described: (1) eye size increases rapidly during ascent of early larval stages from bathypelagic to upper-mesopelagic depths, (2) decreases rapidly in later larval life during descent to postlarval depths, and (3) increases slowly thereafter, accompanying relative diminution of photophores. *Thysanopoda spinicaudata*, which has smaller eyes than *T. cornuta*, though much larger than *T. minyops*, seems to lack abdominal photophores but shows postlarval changes in relative eye size that are similar to the species that possess photophores. These and other adaptations to great depths, such as gill size, are considered.

65. Broda, Hellmuth, Doug Brugge, Keiichi Homma and J. Woodland Hastings (1985). Circadian Communication between Unicells? Effects on Period by Cell-Conditioning of Medium. *Cell Biophysics* 8:47-67.

Populations of *Gonyaulax polyedra*, in two different phases, about 11 hours apart, were mixed and the intensity of their spontaneous bioluminescence glow recorded for about 2 weeks under conditions of constant dim ( $35 \pm 3 \mu\text{E}/\text{m}^2/\text{s}$ ) white light and constant temperature ( $19.0 \pm 0.3^\circ\text{C}$ ). The phases and amplitudes of glow signals recorded from mixed cultures were compared with those obtained from the arithmetic sum of the intensity data from two control vials. Peaks in control cultures generally remained separate, but there was a spontaneous increase in the period beginning 6

to 11 days after the onset of constant conditions. This did not occur in cultures in which the medium was exchanged with fresh medium every 2 days. In the actual mixes of two cultures there was a merging of the two subpeaks in the signal, which did not occur when the medium was exchanged. The results indicated that conditioning of the medium by cells may affect the period of the circadian rhythm and that this might result in a type of communication.

66. Broda, Hellmuth, Van D. Gooch, Walter Taylor, Nick Aiuto and J. Woodland Hastings (1986). Acquisition of Circadian Bioluminescence Data in *Gonyaulax* and an Effect of the Measurement Procedure on the Period of the Rhythm. *J. Biol. Rhythms* 1(3):251-263.

During measurements of the circadian (approximately 24-hour) rhythms of spontaneous bioluminescence in the marine dinoflagellate *Gonyaulax polyedra*, the individual cultures in vials were shielded from otherwise constant dim light for 1 to 3 min every 20 to 60 min by a photomultiplier housing that was moved from vial to vial. The high-frequency dark pulses caused a small but consistent shortening of the free-running circadian period, but there was no indication that the dark pulses caused entrainment. Hardware and software components of the microcomputer-controlled data collection system are described. A microcomputer controlled the movement of the photomultiplier and acquired the data via an analog-to-digital converter. The algorithms distinguished and separately recorded background glow, intermittent flashes and total light from populations ranging in number from  $10^3$  to  $10^5$  cells in volumes from 1 to 10 mL. Fast video display techniques allowed continuous on-line viewing of incoming data, together with a display of the data recorded over the preceding day or two. Detection of mechanical and software errors coupled with recovery systems maintained high reliability of data collection.

67. Broda, Hellmuth and J. Woodland Hastings (1984). Communication of Circadian Time Information in Cultures of *Gonyaulax*? *Eur. J. Cell Biol.*

**ABSTRACT.** Individual cells and populations of *Gonyaulax* initially show no mutual synchronization of circadian rhythms. However, after 7-10 days under constant conditions, mixed populations originally in different phases show merging of the rhythmic peaks and shortening of the free-running period. These

effects are not observed if the medium is replaced frequently during the experiment. Control cultures after 7–10 days show a lengthening of the free-running period, which also does not occur if the medium is repeatedly replaced. These effects suggest the possibility of communication among cells via the medium.

68. Broda, Hellmuth and J. Woodland Hastings (1985). Singularity in a Unicell: Can Pulses of Protein Synthesis Inhibitors Stop the Biological Clock? *Synergetics* (Berlin) 29:222–223.

Inhibitors of protein synthesis on the 80s ribosome and light pulses phase shift the circadian rhythm of bioluminescence in *Gonyaulax*. A singularity in the phase response curve exists that coincides with the transition from a weak to a strong response at the time of largest achievable phase shift. Drug pulses close to this singularity may result in double peaks or abolishment of the rhythm. This effect may be due to slight differences in the effectiveness of the drug on individual cells.

69. Broda, Hellmuth and J. Woodland Hastings (1985). Medium Mediated Effects on Circadian Period Provide Circumstantial Evidence for Communication in *Gonyaulax* Cultures. *Interdiscip. Cycle Res.* 16(2):124.

**ABSTRACT.** The free-running circadian rhythm of bioluminescence in individual cells of the dinoflagellate *Gonyaulax polyedra* shows no mutual synchronization for durations of 7 to 10 days. After this period, however, mixes of populations on different cycles show merging of activity peaks and shortening of the free-running periods. The effects are avoided if the medium is regularly changed. These observations suggest a possible intercellular communication via the medium.

70. Broda, Hellmuth, Walter Taylor and J. Woodland Hastings (1983). Singularity in a Unicell? Can Pulses of Protein Synthesis Inhibitors Stop the Biological Clock? *Interdisziplinäre Tagung über Regulation und Informationsverarbeitung in Pflanzen und Pflanzengesellschaften*.

**ABSTRACT.** Inhibitors of protein synthesis on the 80s ribosome and light pulses phase shift the circadian rhythm of bioluminescence in *Gonyaulax*. A singularity in the phase response curve exists that coincides with the transition from a weak to a strong

response at the time of largest achievable phase shift. Drug pulses close to this singularity may result in double peaks or abolishment of the rhythm. This effect may be due to slight differences in the effectiveness of the drug on individual cells.

71. Broenkow, William W., Alan J. Lewitus, Mark A. Yarbrough and Robert T. Krenz (1983). Particle Fluorescence and Bioluminescence Distributions in the Eastern Tropical Pacific. *Nature* 302:329–331.

Vertical profiles of fluorescence, beam attenuation and bioluminescence in the oxygen minimum zone of the eastern tropical Pacific off central Mexico are related to possible physical and biological particle sources. Fluorescence maxima are reported at 60 m, corresponding with maximum chlorophyll a concentrations, 130 m and between 200 and 400 m, the last being reported for the first time. In this deepest layer,  $\kappa$  correlates directly with fluorescence. The bioluminescence maximum correlates with the shallowest fluorescence maximum and exhibits strong diurnal periodicity. Increased bioluminescence at 50 m but not at 100 m associated with the passage of the deep sonic scattering layer suggests that the increase is due to stimulation of luminous organisms already present at the depth rather than luminescence from organisms comprising the scattering layer.

72. Buck, John B. (1978). Functions and Evolutions of Bioluminescence. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 419–460.

The functions of bioluminescence are considered in terms of individual behavior, coordinated behavior, behavior tailored to the behavior of unrelated kinds of animals and altruistic or group-benefit behavior, instead of the usual categories of predation, avoiding predation and communication, which are subsumed in each of the proposed new categories. Examples of all behaviors are provided. Theories on the origins and evolution of bioluminescence are considered.

73. Buskey, Edward J. (1983). The Effects of Small Scale Patchiness of Phytoplankton on Copepod Swimming Behavior. Ph.D. Dissertation, University of Rhode Island.

The copepod *Pseudocalanus minutus* swims more slowly and pauses more often in the presence of phytoplankton than in their absence. This behavior is

mediated both by chemosensory and mechanosensory receptors. *P. minutus* also exhibits a slight positive response to food gradients, while another copepod, *Acartia hudsonica*, does not. In the presence of luminous dinoflagellates *A. hudsonica* exhibits increased high speed swimming bursts, increased average swimming speeds, more direct swimming paths, and decreased slow speed grazing behavior. These behavioral changes should result in reduced grazing on luminous dinoflagellates, which hypothesis suggests that bioluminescence functions in dinoflagellates to deter predation. These behavioral changes in copepods may be attributed to the light flashes of dinoflagellates and not to any other property such as chemical exudates.

74. Buskey, Edward J., Christopher G. Mann and Elijah Swift (1987). Photophobic Responses of Calanoid Copepods: Possible Adaptive Value. *J. Plankton Res.* 9(5):857-870.

A general pattern of photophobic responses has been observed which differs for calanoid copepods from freshwater, estuarine and oceanic environments. Using a video-computer system for motion analysis, the photophobic responses of light and dark-adapted calanoid copepods were compared. Dark-adapted copepods were exposed to 600-msec flashes of dim blue light at 5-sec intervals which simulated the flashes of bioluminescent marine zooplankton. Light-adapted copepods were exposed to 600-msec intervals of darkness at 5-sec intervals to simulate shadows of organisms passing overhead. Four species of coastal marine copepods (*Acartia hudsonica*, *Centropages hamatus*, *Pseudocalanus minutus* and *Temora longicornis*) all showed photophobic responses to both flashes and shadows. These responses may have adaptive value to the copepods since they live in an environment with predators that are bioluminescent at night and cast shadows on their prey during the day (e.g., ctenophores and cnidarian medusae). Two species of oceanic copepods (*Euchaeta marina*, *Pleuromamma abdominalis*) showed strong photophobic responses to flashes but no response to shadows. This may correspond to the abundance of bioluminescent predators on copepods in the oceanic environment (fish, ctenophores, siphonophores, etc.) and their lack of exposure to the shadows of predators, since both these species are rarely found in the euphotic zone

during the day. Two species of freshwater copepods (*Daipomus sanguineus*, *Epishura massachusettsensis*) showed no similar photophobic response to flashes of light. This lack of startle response may relate to the lack of bioluminescence in the freshwater environment. Freshwater copepods showed a weak photophobic response to shadows. The adaptive value of this behavior is unclear, however, since the responses seem to be too weak to function for escape, and the dominant predators large enough to cast shadows (fish) tend to approach their prey laterally.

75. Buskey, Edward J., Lesley Mills and Elijah Swift (1983). The Effects of Dinoflagellate Bioluminescence on the Swimming Behavior of a Marine Copepod. *Limnol. Oceanogr.* 28(3):575-579.

The horizontal swimming patterns of groups of *Acartia hudsonica* were tracked and described using a video-computer system. The patterns were compared in the presence of clones of bioluminescent and non-bioluminescent *Protophycolax tamarensis*. Bioluminescent dinoflagellates increased the number of high-speed swimming bursts by the copepods and thus decreased the amount of slow-speed swimming characteristic of their grazing behavior. With bioluminescent dinoflagellates, swimming paths were less circuitous and swimming speeds higher. This behavior may tend to move copepods away from bioluminescent dinoflagellates in nature. Both changes in swimming behavior should result in reduced grazing by the copepods on bioluminescent dinoflagellates.

76. Buskey, Edward J., George T. Reynolds, Elijah Swift and Alan J. Walton (1985). Interactions between Copepods and Bioluminescent Dinoflagellates: Direct Observations Using Image Intensification. *Biol. Bull.* 169(2):530.

**ABSTRACT.** Observations using image intensification indicate that little bioluminescence is stimulated in dinoflagellates by copepod swimming but that intense bioluminescence results from copepod feeding. Interactions between individual copepods and single dinoflagellates result in bright, sometimes pulsating flashes lasting one second or longer and rapid swimming by the copepod away from the flash. This observation that a single dinoflagellate can disrupt the feeding activity of a copepod suggests that dinoflagellate bioluminescence functions as a defense against predation.

77. Buskey, Edward J. and Elijah Swift (1983). Behavioral Responses of the Coastal Copepod *Acartia hudsonica* (Pinhey) to Simulated Dinoflagellate Bioluminescence. *J. Exp. Mar. Biol. Ecol.* 72:43-58.

Light pulses were used to mimic dinoflagellate bioluminescence and test its effects on the swimming behavior of *Acartia hudsonica* (Pinhey). The horizontal swimming patterns of the copepods were tracked and described using a video-computer system. Single flashes of light of 60-msec duration, with a wavelength of peak emission of 475 nm and an intensity of  $2 \text{ E}\mu\text{m}^{-2} \text{ s}^{-1}$  caused a "startle" response consisting of a short burst of high speed swimming. A series of these flashes repeated every 5 sec resulted in higher average swimming speed, more swimming speed bursts and straighter paths. These behavioral changes are similar to those previously found for *A. hudsonica* in the presence of bioluminescent dinoflagellates. The effects of altering the intensity, duration and color of the simulated dinoflagellate flash were also tested. Our results support the hypothesis that dinoflagellate bioluminescence is a highly evolved adaptation for repelling nocturnal grazers.

78. Buskey, Edward J. and Elijah Swift (1983). Behavioral Responses of Oceanic Zooplankton to Simulated Bioluminescence. *EOS* 64(52):1044.

**ABSTRACT.** Some dark-adapted zooplanktonic species exhibit much greater startle responses to simulated bioluminescent flashes than others. In particular, the luminous copepod *Metridia longa* is much more responsive than the nonluminous copepod *Calanus finmarchicus*. Thus, bioluminescence in *Metridia* may serve as a warning signal as well as a defense against predation.

79. Buskey, Edward J. and Elijah Swift (1985). Behavioral Responses of Oceanic Zooplankton to Simulated Bioluminescence. *Biol. Bull.* 168(2):263-275.

A defensive function often has been suggested for the bioluminescence of dinoflagellates and copepods, but there is only limited experimental evidence. Using closed circuit television equipment and infrared illumination, the behavioral responses of planktonic copepods, ostracods, polychaetes, chaetognaths and euphausiids to simulated bioluminescent flashes were recorded. The swimming patterns of these organisms were then quantified using a video-computer system for motion analysis (the Bugwatcher). The

photophobic response exhibited by certain copepod species in response to simulated dinoflagellate flashes, as well as the lack of response by several potential predators on copepods to their simulated bioluminescence, provide new insight into the roles of bioluminescence in plankton ecology. Comparison of the responses of the nonbioluminescent copepod *Calanus finmarchicus* and the bioluminescent copepod *Metridia longa* to simulated copepod bioluminescence show that *Metridia* is much more responsive than *Calanus*. This suggests that bioluminescence in *Metridia* may be recognized as a warning signal by conspecifics in addition to serving as a defense against predation.

80. Buskey, Edward J. and Elijah Swift (1986). Behavioral Attributes Affecting Vertical Distribution of the Bioluminescent Copepod *Pleuromamma xiphias*. *Biowatt News* 3:7 (April).

Copepods of the genus *Pleuromamma* are responsible for much of the nocturnal epipelagic bioluminescence of the Sargasso Sea. *P. xiphias* is found to be negatively phototactic at all light intensity levels. The daytime depth distribution corresponds to the threshold light intensity for negative phototaxis and the nighttime depth distribution encompasses the depth of the chlorophyll maximum. These observations suggest that light and food concentration may play important roles in the vertical distribution and movements of this species.

81. Buskey, Edward J. and Elijah Swift (1987). Prediction of Natural Bioluminescence in the Sargasso Sea Using an Encounter Model. *EOS* 68(50):1695.

**ABSTRACT.** Bioluminescence in the Sargasso Sea is produced mainly by crustaceans, larvaceans and dinoflagellates in response to mechanical disturbances by other organisms and may function as a defense mechanism to deter predation. Using the swimming speeds of luminous zooplankton, the distribution of swimming speeds for a mixed population of other zooplankton and estimates of the encounter radius to predict the number of encounters and assuming every encounter produces a flash that is about 10% of the total stimutable capacity of the flashing organism, a model has been developed to predict total background bioluminescence per cubic meter per second.

82. Buskey, Edward J., Elijah Swift and Raymond C. Smith (1985). Behavioral Attributes Affecting Vertical

Distribution of the Bioluminescent Oceanic Copepod *Pleuromamma xiphias*. *EOS* 66(51):1313.

**ABSTRACT.** An action spectrum of phototaxis was determined for *Pleuromamma xiphias*, a copepod of the genus responsible for much of the nocturnal epipelagic bioluminescence in the Sargasso Sea and it was found to be negatively phototactic at all intensities eliciting a response. This datum, along with data on surface light intensity, light transmission through the water and copepod swimming speeds, could allow prediction of daytime depth distributions. At night, *P. xiphias* turns more frequently and swims more slowly near the chlorophyll maximum than at greater depths. This behavioral change may cause them to spend more time near the chlorophyll maximum during their vertical migration.

83. Butcher, S., P. N. Dilly and Peter J. Herring (1982). The Comparative Morphology of the Photophores of the Squid *Pyroteuthis margaritifera* (Cephalopoda:Enoploteuthidae). *J. Zool.* (London) 196:133-150.

*Pyroteuthis margaritifera* has morphologically distinctive photophores on the tentacles, eyeball and in the mantle cavity. The photogenic tissue in each photophore is identical, has a blue-green fluorescence and luminesces on treatment with dilute hydrogen peroxide. The photocytes frequently contain organized fibrillar material akin to that in the photocytes of certain other cephalopods. Several different types of blood vessel are present among the photocytes, including some, apparently restricted to the photophores, with a microvillous endothelium. Haemocyanin is present not only within identifiable blood vessels but also in some intercellular spaces. On the basis of their characteristic optical systems the photophores can be separated into three types: (1) tentacular; (2) ocular and anal; (3) branchial and median abdominal. The tentacular photophores have collagenous reflector and light guide systems and the median ones are double organs. The ocular and anal organs do not have collagenous optical structures but an elaborate variety of reflective iridosomes. Those in the aperture of the photophores appear to act as interference filters. The branchial and abdominal organs have iridosomes as the major reflective tissue but collagenous fibrils function as light guides in the aperture of these organs and their emission is diffuse rather than collimated.

84. Byers, David M. and Edward A. Meighen (1984). *Vibrio harveyi* Aldehyde Dehydrogenase. Partial Reversal of Aldehyde Oxidation and Its Possible Role in the Reduction of Fatty Acids for the Bioluminescence Reaction. *J. Biol. Chem.* 259(11):7109-7114.

*Vibrio harveyi* aldehyde dehydrogenase, which catalyzes the oxidation of long chain aliphatic aldehydes to acids, has been discovered to have both acyl-CoA reductase and thioesterase activities. Tetradecanoyl-CoA was reduced to tetradecanal in the presence of NAD(P)H, as monitored by the stimulation of luciferase activity by the aldehyde product (acyl-CoA reductase). In the absence of NADPH, [<sup>3</sup>H]tetradecanoyl-CoA was hydrolyzed to the hexane-soluble fatty acid (thioesterase). Inhibition data with N-ethylmaleimide suggest that a single active site on aldehyde dehydrogenase is responsible for all three enzymatic activities. The acyl-CoA reductase activity was maximal at low NADPH concentration (about 1  $\mu$ M), whereas much higher concentrations of NADH (>100-fold) were required for optimal activity. Further increases in NADPH or NADH concentrations inhibited both the acyl-CoA reductase and thioesterase reactions. On the basis of the specificity of aldehyde dehydrogenase for NADP(H), an improved purification procedure employing affinity chromatography on 2',5'-ADP-Sepharose is described. Although fatty acid reductase activity could not be reconstituted, aldehyde dehydrogenase specifically stimulated the rate of acylation of the acyl protein synthetase component from the *Photobacterium phosphoreum* fatty acid reductase system. This observation, combined with the partial reversal of aldehyde oxidation described above, suggests a possible role of aldehyde dehydrogenase in aldehyde biosynthesis for the luminescent reaction in *V. harveyi*.

85. Byers, David M., Angel Rodriguez, Luc M. Carey and Edward A. Meighen (1986). Bioluminescence-Related Acyltransferases from *Photobacterium phosphoreum* and *Vibrio harveyi*. In *Bioluminescence and Chemiluminescence Part B.*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press (*Methods Enzymol.* 133:183-188).

Acyl-CoA acyltransferase enzymes catalyze the generation of fatty acids (possibly from acyl-acyl-carrier protein as a precursor) for reduction into the long-chain aldehyde substrate involved in the bacterial

bioluminescence reaction in *P. phosphoreum* and *V. harveyi*. These enzymes appear to be induced during the midexponential growth phase.

86. Campbell, Anthony K., Maurice B. Hallett, Richard A. Daw, Malcolm E. T. Ryall, Russell C. Hart and Peter J. Herring (1981). Application of the Photoprotein Obelin to the Measurement of Free  $\text{Ca}^{2+}$  in Cells. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 601-607.

*Obelia geniculata*, a hydroid which produces the  $\text{Ca}^{2+}$ -activated photoprotein obelin, is found off the coasts of the United Kingdom. In addition, the colonial radiolarian *Thalassicola*, found off the west coast of Ireland, also produces a  $\text{Ca}^{2+}$ -activated photoprotein. When stimulated mechanically or chemically, it emits a flash of light with a peak emission wavelength of 440 nm. Luminescence is inhibited by  $\text{Mg}^{2+}$  and  $\text{Na}^+$  and atmospheric oxygen is not required for the reaction. Spent obelin and thalassicolin can be reactivated by synthetic coelenterazine. Thus it is concluded that luminous radiolarians contain a  $\text{Ca}^{2+}$ -activated photoprotein similar to that found in coelenterates, and either may be substituted for aequorin in intracellular  $\text{Ca}^{2+}$  measurements.

87. Campbell, Anthony K. and Peter J. Herring (1987). A Novel Red Fluorescent Protein from the Deep Sea Luminous Fish *Malacosteus niger*. *Comp. Biochem. Physiol.* 86B(2):411-417.

A protein, blue in daylight and red fluorescent under ultraviolet (366 nm) light, has been extracted and partially purified from the red-emitting suborbital luminous organ of the deep sea fish *Malacosteus niger*. The protein had a molecular weight on G-100 Sephadex of approx. 32,000 and on SDS polyacrylamide gel electrophoresis of approx. 30,000. The absorbance maxima of the isolated protein were at 555 nm and 612 nm. There were four fluorescence excitation maxima (305, 332, 374 and 392 nm) corresponding to two emission maxima (564 and 626 nm; 564 nm for 305 nm and 374 nm and 626 nm for 332 nm and 392 nm). The protein exhibited a low intensity phosphorescence after exposure to visible light. The chromophore appeared to be covalently bound, some being extracted in acid methanol at 0°C

or in boiling methanol. The protein has characteristics similar to a phycobili protein, previously found only in blue-green and red algae. Similar, but not identical, proteins were also isolated from two other related stomiatoid fishes, *Aristostomias* and *Pachystomias*.

88. Cao, Yunhiu and K. Hu (1981). Distribution and Composition of Luminous Bacteria in Estuary of Yangtse River. *Practice of Oceanography* 13:65-68 (Chinese).

This paper was not available for review.

89. Cao, Yunhiu, K. Hu and S. Wang (1979). Preliminary Studies of Luminous Bacteria from the East China Sea. *Practice of Oceanography* 4:24-30 (Chinese).

This paper was not available for review.

90. Carey, Luc M., Angel Rodriguez and Edward A. Meighen (1984). Generation of Fatty Acids by an Acyl Esterase in the Bioluminescent System of *Photobacterium phosphoreum*. *J. Biol. Chem.* 259(16):10,216-10,221.

The fatty acid reductase complex from *Photobacterium phosphoreum* has been discovered to have a long chain ester hydrolase activity associated with the 34K protein component of the complex. This protein has been resolved from the other components (50K and 58K) of the fatty acid reductase complex with a purity of >95% and found to catalyze the transfer of acyl groups from acyl-CoA primarily to thiol acceptors with a low level of transfer to glycerol and water. Addition of the 50K protein of the complex caused a dramatic change in specificity increasing the transfer to oxygen acceptors. The acyl-CoA hydrolase activity increased almost 10-fold, and hence free fatty acids can be generated by 34K protein when it is present in the fatty acid reductase complex. Hydrolysis of acyl-S-mercaptoethanol and acyl-1-glycerol and the ATP-dependent reduction of the released fatty acids to aldehyde for the luminescent reaction were also demonstrated for the reconstituted fatty acid reductase complex, raising the possibility that the immediate source of fatty acids for this reaction in vivo could be the membrane lipids and/or the fatty acid synthetase system.

91. Case, James F. (1979). Bioluminescence Mechanisms. Progress Report Abstracts. Oceanic

Biology. Office of Naval Research, Washington, D.C., Report ONR-ACR-230, pp. 17-18.

**ABSTRACT.** The luminous midshipman fish *Porichthys* may derive its luciferin by ingestion of the ostracod crustacean *Vargula tsujii*. The organs of Pesta and eyestalks of the shrimp *Sergestes* detect and compensate for body inclination in determining the direction of counter-illuminating light emission. Since the first flash of bioluminescence from the dinoflagellate *Pyrocystis* after entering darkness is much brighter than subsequent flashes, a handling apparatus has been developed to avoid inadvertent stimulation during study.

92. Case, James F. (1981). Lanternfish as Examples of Macroscopic Light Sources in the Ocean. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis (Minnesota): Burgess Publishing Co., pp. 134-138.

The vertical distribution and patchiness, luminous organs, emission kinetics, intensity, response to stimulation and control mechanisms of myctophids are discussed. It is argued that their contribution to the light budget should be assessed and incorporated into any proposed bioluminescence models.

93. Case, James F. (1982). Bioluminescence Mechanisms. In *Progress Report Abstracts*, Office of Naval Research, Washington, D.C., December, pp. 25-26.

**ABSTRACT.** A fast spectrometer system has been developed and tested on shipboard and is described. Using this system spectra have been obtained at sea from about 40 species. Luminescence in specimens of *Gnathophausia* which have lost their luminescence ability in the laboratory may be restored by feeding upon fresh *Triphoturus mexicanus*, a myctophid. Bioluminescence in the worm *Chaetopterus* is associated with ejection of water contained in its tube. Investigations of counterillumination in the shrimp *Sergestes* and microsources in *Pyrocystis* are underway.

94. Case, James F. (1982). Bioluminescence Mechanisms. In ONR Oceanic Chemistry and Biology Group Program Science Report, Office of Naval Research, Washington, D.C., 1 March, pp. V-15-V-16.

**ABSTRACT.** An image intensifier system with a light gain of  $10^6$  has been completed and is in use.

Bioluminescence in juveniles of the fish *Porichthys* can be completely discharged and restored by feeding on the ostracod crustacean *Vargula tsujii*. This fact suggests that the fish requires an exogenous luciferin source. On the other hand, luminescence in the mysid shrimp *Gnathophausia* appears not to depend on a specific dietary requirement for luciferin, but to be nonspecifically related to nutritional state. Studies of counterillumination by the shrimp *Sergestes* indicate that luminescence does not effectively eliminate the silhouette. Luminescent microsource coordination and properties in the dinoflagellate *Pyrocystis* are being studied.

95. Case, James F. and Linda G. Strause (1978). Neurally Controlled Luminescent Systems. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 331-366.

Mechanisms for regulation of light emission in multicellular animals include mechanical shuttering or filtering, secretion of luminous system components into the surrounding water to produce light upon mixing and direct neural action upon intrinsic light-producing systems. This chapter concentrates on the last of these mechanisms, specifically upon identification of the light sources, the physical relationship of the light sources to the controlling innervation, the neural transmitter process and the means by which neural excitation triggers light emission. Emphasis is upon fireflies, but fish (*Porichthys* and myctophids), coelenterates (*Renilla*, *Mnemiopsis* and various hydrozoans), worms (polychaetes) and echinoderms (ophiuroids) are discussed in some detail. Neural control is suggested for the tunicates, hemichordates, crustaceans and molluscs, but little is known. A unified control mechanism involving calcium regulation is suggested.

96. Case, James F., Edith A. Widder, S. A. Bernstein, Michael I. Latz, D. P. Cook and Mark R. Bowlby (1987). Quantitative Measurement of Marine Bioluminescence. *EOS* 68(50):1695.

**ABSTRACT.** A new form of bathyphotometer in which a defined excitatory stimulus is applied at an entrance grid to organisms carried in a high-volume stream through a meter-long detection chamber has been designed and evaluated both at sea and in the laboratory in comparison with other in situ bathyphotometers. Flash kinetics, total flash energy and emission spectra have been successfully measured.

97. Charbonneau, Harry, and Milton J. Cormier (1979).  $\text{Ca}^{2+}$ -induced Bioluminescence in *Renilla reniformis*. Purification and Characterization of a Calcium-triggered Luciferin-binding Protein. *J. Biol. Chem.* 254(3):769-780.

A  $\text{Ca}^{2+}$ -triggered luciferin-binding protein (BP-LH<sub>2</sub>) from the bioluminescent marine coelenterate, *Renilla reniformis*, has been purified by conventional methods. One kilogram of processed animals yields approximately 2.7 mg of pure protein with an overall yield of 55%. Physicochemical studies show that BP-LH<sub>2</sub> is a globular protein containing one single polypeptide chain with one disulfide bond. Ultracentrifugation studies, amino acid analysis, and sodium dodecyl sulfate-gel electrophoresis show that BP-LH<sub>2</sub> has an average molecular weight of 18,500. BP-LH<sub>2</sub> has a Stokes radius of 23 Å, a sedimentation coefficient,  $S_{20,w}^0$  of 2.3 S, and an isoelectric point of 4.3. The acidic nature of the protein was confirmed by amino acid analysis, which showed that 27% of the residues are acidic. The protein contains no carbohydrate, phosphate, or tryptophan. There is one noncovalently bound molecule of coelenterate type luciferin resulting in distinct protein spectral properties with absorption maxima at 276 nm ( $\epsilon_{276}^{0.1\%} = 1.31$ ) and 446 nm ( $\epsilon_{446}^{0.1\%} = 0.47$ ) and a fluorescence emission at 520 nm (uncorrected). In the presence of  $\text{Ca}^{2+}$ , BP-LH<sub>2</sub> will react with *Renilla luciferase* to give the characteristic in vitro blue bioluminescence.  $\text{Ca}^{2+}$  binding produces a distinct change in the spectral properties of BP-LH<sub>2</sub>, including a four-fold enhancement of tyrosine fluorescence at 332 nm and a five-fold fluorescence enhancement at 520 nm. In addition, the visible absorption maximum shifts from 446 nm to 420 nm. The fluorescence enhancement at 320 nm occurs over the range from 1 to 10  $\mu\text{M}$   $\text{Ca}^{2+}$ . BP-LH<sub>2</sub> has two  $\text{Ca}^{2+}$ -binding sites with an estimated  $K_d$  of 0.02  $\mu\text{M}$ , in 10 mM Tris at pH 7.2. BP-LH<sub>2</sub> was compared to several well studied  $\text{Ca}^{2+}$ -binding proteins and was found to possess similar  $\text{Ca}^{2+}$ -binding and physicochemical properties. This study clearly demonstrates that BP-LH<sub>2</sub> is capable of triggering a bioluminescent flash in response to an intracellular  $\text{Ca}^{2+}$  transient.

98. Christophe, B. and Fernand Baguet (1981). Adrenergic Control of Isolated Photocytes from *Porichthys* Photophores. *Arch. Int. Physiol. Biochem.* 89:P20-P21.

**ABSTRACT.** The neurotransmitters epinephrine and norepinephrine stimulate light emission in photocytes isolated from the fish, *Porichthys notatus*. Norepinephrine elicits a rapid response (completed within 1 min of stimulation) whose intensity increases with increasing concentration from  $10^{-7}$  to  $10^{-3}$  M. Epinephrine elicits two responses, one similar to the norepinephrine response, the other a slower glow lasting about 19 min.  $\alpha$ - and  $\beta$ -adrenergic antagonists have mixed effects. The observations suggest control of the rapid luminescence by norepinephrine and the slow luminescence by epinephrine.

99. Christophe, B. and Fernand Baguet (1982). Potassium Cyanide Stimulation of Isolated Photocytes from a Luminescent Fish. *Arch. Int. Physiol. Biochem.* 40:P10-P11.

**ABSTRACT.** Adrenaline induces two types of luminescent response in photophores isolated from the fish *Porichthys notatus*, a fast response and a slow response about half as intense as the fast response. The respiratory metabolic inhibitor KCN also stimulates light emission about three times as bright as the fast response to adrenaline and lasting about 21 min.  $\alpha$ -adrenergic antagonists block the adrenaline response but do not affect the KCN response.  $\beta$ -adrenergic antagonists greatly inhibit the KCN response but have little effect on the adrenaline slow response.  $\text{MnCl}_2$ , which blocks inward  $\text{Ca}^{2+}$  current, does not affect the KCN response but inhibits both adrenaline responses. These results suggest different stimulatory mechanisms for KCN and adrenaline.

100. Christophe, B. and Fernand Baguet (1982). Luminescence of Isolated Photophores and Supracaudal Gland from *Myctophum punctatum*: Electrical Stimulation. *Comp. Biochem. Physiol.* 71A:131-136.

Isolated photophores of the living bathypelagic fish *Myctophum punctatum* respond to train of weak (10 to 25 V) and short (2 to 5 msec) electrical stimuli applied at different frequencies (8 to 100/sec) by a luminous response. This response is characterized by a short emission latency time, the peak of light develops within about 2 sec after the beginning of the electrical stimulation: afterwards the light decreases to a constant level within about 8 sec. Stimuli of higher strength (60 to 75 V) and longer duration (8 to 16 msec) applied at different rates (1 to 100/sec) evoke brief flashes. The isolated supracaudal gland

emits flashes in response to electrical stimulation whatever the strength and the duration of stimuli. The flash of the supracaudal gland differs from the flash of the isolated photophores in three respects: lower threshold, higher magnitude and longer duration.

101. Christophe, B. and Fernand Baguet (1983). Luminescence of Isolated Photocytes from *Porichthys* Photophores: Adrenergic Stimulation. *J. Exp. Biol.* 104:183-192.

A fast transient peak of light, followed by a slow luminescence, was produced by isolated photophores of *Porichthys notatus* when exposed to 1 mM-epinephrine, norepinephrine or phenylephrine, an  $\alpha$ -adrenergic agonist. Only a slow luminescence was induced by 1 mM-isoproterenol, the  $\beta$ -adrenergic agonist. After removal of the reflector and surrounding tissues, the isolated photogenic cells—i.e., the photocytes—responded to norepinephrine and phenylephrine by producing a fast transient peak of light and to isoproterenol by a slow luminescence. Epinephrine evoked both types of luminescence. The emission latency time, the amplitude and the total duration of the light responses were significantly less than those of the photophore. The results suggest that both epinephrine and norepinephrine combine with sympathetic  $\alpha$  or  $\beta$  receptors upon the photocytes to trigger light production.

102. Christophe, B. and Fernand Baguet (1985). Seasonal Variations of Luminescence in Photophores of *Porichthys notatus* (Teleostei: Bactrachoididae). *Ann. Soc. R. Zool. Belg.* 115(2):197-201.

The present observations demonstrate the seasonal variation of luminescence in light organs isolated from the epipelagic fish *Porichthys notatus*. The light production is maximal at the end of the summer and at the beginning of autumn: it is minimal during the winter. This fish breeds in the summer (from June to August). The role of the bioluminescence in courtship and nestguarding by the male is discussed.

103. Cigala-Fulgosi, F. and G. Gandolfi (1983). Re-description of the External Morphology of *Somniosus rostratus* (Risso, 1826) with Special Reference to Its Squamation and Cutaneous Sensory Organs and Aspects of Their Functional Morphology (Pisces Selachii Squalidae). *Monitore Zool. Ital.* (N.S.) 17:27-70.

The lack of luminescence in the shark *Somniosus rostratus* is documented. Early reports of luminous organs mistook the pit organs for photophores.

104. Cohen, Anne C. and James G. Morin (1986). Three New Luminescent Ostracodes of the Genus *Vargula* (Myodocopida, Cypridinidae) from the San Blas Region of Panama. *Contrib. Sci. Nat. Hist. Mus. Los Angeles Co.* 373:1-23.

Three new species of luminescent myodocopid ostracodes, *Vargula graminicola*, *V. shulmanae* and *V. contragula* from the San Blas Islands, Panama, are described. *V. graminicola* and *V. shulmanae* are sibling species differing in few morphological characters but distinctive in diet, habitat and bioluminescent patterns. They are compared to *Vargula parasitica* (Wilson, 1913), a morphologically similar Jamaican ostracode. *V. contragula* is morphologically a very distinct species. All three new species produce distinctive bioluminescent patterns in the water column at night. *V. graminicola* occurs within and above shallow marine seagrass beds; *V. shulmanae* occurs primarily within and over steep slopes and walls of deeper coral reefs; and *V. contragula* is found mainly on gorgonian-dominated, shallow, low-profile coral reefs and slopes.

105. Cohn, Daniel H. (1983). Isolation, Organization, and Expression of the Luciferase Genes from *Vibrio harveyi*. Ph.D. Dissertation, University of California, San Diego.

Induction of bioluminescence in *Vibrio harveyi* is regulated by nutrients including carbon (catabolite repression), nitrogen (arginine), and iron. Upon induction of luminescence bacterial luciferase, among other enzymes, is synthesized. The genes encoding bacterial luciferase, *lux A* and *lux B*, were isolated and their geometry, along with part of a third gene, in a *lux* operon determined. Studies on RNA suggested control at the level of transcription.

106. Cohn, Daniel H., Gary B. Leisman and Kenneth H. Nealson (1979). Detection and Characterization of Bacterial Luciferases in Symbioses Containing Non-Culturable Bacteria. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 71.

**ABSTRACT.** Bacteria cannot be cultured from the light organs of many fish and squid, such as members of the family Anomalopidae, even though

other evidence strongly suggests the presence of symbiotic luminous bacteria in these organs. However, bacterial luciferase is unique to luminous bacteria and can be used as an indication of their presence. Thus, bacterial luciferase exhibiting slow kinetics has been extracted from light organs of all three members of the family Anomalopidae, while bacterial luciferase exhibiting fast kinetics has been extracted from a variety of angler fish and the midwater squid *Heteroteuthis hawaiiensis*.

107. Colfax, G., Till Roenneberg and J. Woodland Hastings (1987). A Possible Model System for Cell Behavior in Red Tides: Aggregation and Passive Sedimentation Occur as an Endogenous Active Circadian Rhythm in *Gonyaulax polyedra*. *Int. Symp. Red Tides*.

**ABSTRACT.** *Gonyaulax polyedra* cells during photophase form a complex aggregate, in which they move downward in the center, then swim upward and outward. In scotophase they become inactive and sink. This behavior is controlled by an endogenous circadian clock, with a free-running period of about 22 hours at 20°C, entrainable to 24 hours by light-dark cycles. This cycle may be related to vertical migration and patch formation in red tides and thus may provide the basis for a model system.

108. Colin, Patrick L., Deborah W. Arneson and William F. Smith-Vaniz (1979). Rediscovery and Redescription of the Caribbean Anomalopid Fish *Kryptophanaron alfredi* Silvester and Fowler (Pisces: Anomalopidae). *Bull. Mar. Sci.* 29(3):312-319.

The Caribbean anomalopid fish *Kryptophanaron alfredi* is redescribed from one specimen collected off western Puerto Rico at 200-m depth, and six specimens from Grand Cayman Island taken in 30- to 36-m depths. These specimens differ from the original description in lacking vomerine teeth and in having only two anal spines. Live specimens are now being maintained in aquaria. White scales at the bases of the second dorsal and anal fins may serve as "reflectors." The species is easily distinguished from its eastern Pacific relative *K. harveyi* Rosenblatt and Montgomery, in having more ventral scutes (7 to 9 versus 13) and smaller scales (ca. 120 to 140 scale rows along the back vs. ca. 80).

109. Collier, A. F., R. J. P. Burnham and Peter J. Herring (1979). A System for the Collection of

Comparative Emission Spectra Suitable for Shipboard Use. *J. Mar. Biol. Assoc. UK* 59:489-495.

A simple data acquisition and control system has been developed for the measurement of the spectral emission from bioluminescent animals. A programmable calculator system is used to control a monochromator and to measure, record and graphically display the results. Results from calibration sources and three animals, two euphausiid and one decapod shrimp, are described with comments on the success of the technique.

110. Cormier, Milton J. (1978). Comparative Biochemistry of Animal Systems. In *Bioluminescence in Action*, Peter J. Herring, ed., Academic Press, New York, pp. 75-108.

Bioluminescence in a number of organisms, primarily marine, is described and compared. Emphasis is placed on similarities in reaction biochemistries and mechanisms. Marine species are divided into two large categories, those species that use coelenterate-type luciferin and those that use *Cypridina*-type luciferin. The fireworm, *Odontosyllis*, and the clam, *Pholas*, are placed in individual categories, since they do not fit in either of the two large groupings. Energy transfer reactions are discussed.

111. Cormier, Milton J. (1981). *Renilla* and *Aequorea* Bioluminescence. In *Bioluminescence and Chemiluminescence, Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., Academic Press, New York, pp. 225-233.

*Renilla* bioluminescence involves three enzymes: luciferase; a green fluorescent protein; and a luciferin binding protein. The characteristics of these enzymes and their roles in the bioluminescence reaction are described. *Aequorea* bioluminescence involves only two components, a calcium-activated photoprotein and a green fluorescent protein. These components are also characterized and compared to the components of *Renilla*, and their roles described.

112. Cornelius, G., Angela Schröder-Lorenz and Ludger Rensing (1985). Circadian-Clock Control of Protein Synthesis and Degradation in *Gonyaulax polyedra*. *Planta* 166:365-370.

In growing cultures of the dinoflagellate, *Gonyaulax polyedra*, total protein synthesis showed a

circadian rhythm with a maximum during the phase of the cycle which corresponded to the previous darktime. The maximum coincided with the maximal phase shift of the glow rhythm caused by lower concentrations of the antibiotic anisomycin. The dose responses of inhibition of protein synthesis correlated well with the phase shifting by anisomycin. The amplitude and level of the total-protein synthesis rhythm increased with the growth rate, indicating that the majority of proteins controlled by the circadian clock were cell cycle-dependent. The degradation rate showed the same circadian rhythm as the synthesis rate. Slight variations in uptake and pool size of amino acids were not responsible for the rhythm in the protein-synthesis rate.

113. Daniel, A., A. K. Nagabhushanam and S. Chakrapany (1979). On Bioluminescent *Noctiluca* Swarms Associated with the Movement of Extensive Shoals of Flying-Fishes and Schools of Dolphins in the Northern Arabian Sea in February, 1974. *Rec. Zool. Surv. India* 75:237-246.

A large bluish-green bioluminescent display caused by swarming of the dinoflagellate *Noctiluca miliaris* was observed the nights of 17-18 and 18-19 February 1974 in the northern Arabian Sea during the oceanographic expedition of the INS *Darshak*. The bioluminescence was associated with the movements of shoals of flying-fishes and schools of dolphins. During the day the sea appeared dark green in color. The bloom had disappeared when the area was revisited from 23 to 28 February, leaving no evidence of dead, decaying, or floating fishes or other organisms. Although *Noctiluca* dominated plankton samples taken during the display, other luminous dinoflagellates and zooplankton were found as well.

114. Danilov, V. S. (1979). On the Mechanism of Bioluminescence of Bacteria. *Dokl. Akad. Nauk SSSR Ser. Biophys.* 249(2):477-479 (Russian) :196-198 (English).

A mechanism for bacterial bioluminescence, which must be validated through experimental testing, is proposed. This hypothesis elucidates many characteristics and properties of luciferase. In particular, inconsistencies in previously reported molecular weights, variations in sensitivity of the bacterium to various chemical compounds, reaction intermediaries, and excitation of luciferase by light are explained. It is suggested that the function of bacterial

luciferase is not so much to generate light as to protect the cell from toxic compounds.

115. Danilov, V. S. (1985). Effects of Phenobarbital on Bacterial Luciferase of *Photobacterium fischeri*. *Microbiology (USSR)* 54(4):587-591 (Russian) :468-472 (English).

The effects of phenobarbital on the bioluminescence of marine bacteria *Photobacterium fischeri* and bacterial luciferase were studied. It was shown that the interaction of phenobarbital with the terminal component of luciferase, cytochrome P-450, induces a typical spectral transition with maximum around 380 nm and minimum 420 nm. The binding of phenobarbital to cytochrome prevents the interaction of the latter with the substrate of the luminescent reaction—an aliphatic aldehyde. This mechanism explains the effect of inhibition of bacterial luminescence.

116. Danilov, V. S., N. A. Baranova, A. D. Ismailov and N. S. Egorov (1982). The Effect of Camphor on Bacterial Bioluminescence. *Eur. J. Appl. Microbiol. Biotechnol.* 14:125-129.

The inhibitory effect of camphor on bioluminescence of both bacteria and bacterial luciferase has been examined. The camphor has been shown to be a substrate of cytochrome P-450 of the luminous bacteria *Photobacterium fischeri*. The inhibition of the luminescence reaction provided evidence for the competitive nature of the interaction of camphor and aliphatic aldehyde at the binding site for luciferase. Camphor is also supposed to interact with P-450. The findings indicate that the hydroxylation process of camphor affects the kinetics of the luminescence.

117. Danilov, V. S. and N. S. Egorov (1981). A Multienzyme Model for Bacterial Luciferase. *Bioorgan. Khim.* 7(11):1605-1626 (Russian).

Different hypotheses on the structure and mechanism of bacterial luciferase functioning have been examined and a new model has been suggested which can better fit all the experimental data. In terms of this model, luciferase is regarded not as an individual enzyme, but as a complex made of the three structural components: flavoprotein, an Fe-S-containing protein, and cytochrome P-450. A possible sequence of reactions leading to the light

emission is proposed and functional significance of bacterial luciferase is discussed.

118. Danilov, V. S., A. D. Ismailov and N. A. Baranova (1985). The Inhibition of Bacterial Bioluminescence by Xenobiotics. *Xenobiotica* 15(4):271-276.

The effect of various xenobiotic substrates of microsomal cytochrome P-450, including dimethylaniline, ethylmorphine, hexabarbital and aminopyrine, on the bioluminescence of the bacteria *Vibrio fischeri* and the bacterial luciferase mixed-function oxidase system is described. These compounds are effective inhibitors of the luminescence reaction. The inhibition provided evidence for the competitive nature of the interactions between xenobiotics and an aliphatic aldehyde, which is a substrate of bacterial luciferase, at the binding site for cytochrome P-450. The bioluminescence method is suitable for the analysis of metabolism and detoxication of various xenobiotics.

119. Danilov, V. S., A. D. Ismailov, Yu. A. Malkov and N. S. Egorov (1981). Interaction of Aliphatic Aldehyde with Cytochrome P-450 in Reactions of Bacterial Luminescence. *Bioorgan. Khim.* 7(1):68-74 (Russian).

An aldehyde-binding component of the luminescent bacteria *Photobacterium fischeri* has been identified. It is shown that aliphatic aldehyde participates in the oxidation chain of pyridine nucleotides and binds to a mixed-function oxidase-cytochrome P-450. The binding constant for aldehyde-cytochrome P-450 complex determined by a spectral method turned out equal to Michaelis constant for the luminescence reaction of bacterial luciferase. The substrates, including aliphatic hydrocarbons, and the inhibitors of mixed-function oxidases manifested a competitive inhibition with aldehyde. Some peculiarities of cytochrome P-450 functioning in bacterial luminescence were discussed using decane and decanal as examples.

120. Danilov, V. S. and Yu. A. Malkov (1984). Bacterial Luciferase from *Beneckea harveyi*, an Iron-Containing Enzyme. *Dokl. Akad. Nauk SSSR Ser. Biokhim.* 275(1):206-209 (Russian) :115-118 (English).

Three theories on the nature and structure of the bacterial luciferase molecule and its role in the light-emitting system are presented. One of these, Danilov's hypothesis, requires that bacterial luciferase contain iron ions. Since previous research had drawn negative conclusions regarding the iron requirements of luciferase, the validity of this theory was in question. This paper demonstrates inhibition of luciferase by o-phenanthroline, a ferrous iron chelator, and attributes that inhibition to its binding with iron. It also demonstrates the presence of ferric iron in luciferase. These data support Danilov's hypothesis.

121. Danilov, V. S. and Yu. A. Malkov (1985). Nonheme Iron in Bacterial Luciferase Reaction. *Biochemistry (USSR)* 50(2): 264-269 (Russian): 223-228 (English).

The interaction of bacterial luciferases from *Photobacterium fischeri* and *Beneckea harveyi* with the metal-chelating agent o-phenanthroline was investigated. It was found that o-phenanthroline effectively inhibits the luciferase reaction by binding to the nonheme iron. The influence of various reducing agents on the degree and rate of formation of the colored  $\text{Fe}^{+2}(\text{OP})_3$  complex was studied by the spectral method. It was concluded that nonheme iron is present in bacterial luciferase and is involved in the bioluminescent reaction.

122. Danilov, V. S. and Yu. A. Malkov (1986). Bacterial Luciferase as a Heme-Dependent Monooxygenase. *J. Bioluminescence Chemiluminescence* 1(2):94.

**ABSTRACT.** Bacterial luciferase activity is inhibited by (1) ferricytochrome c (whose reduction depends on flavin); (2) electron acceptors such as ferricyanide, dichlorophenolindophenol and neotetrazolium; (3) heme ligands such as cyanide, azide and CO; and (4) specific cytochrome P-450 inhibitors, such as metyrapone and SKF 525-A and P-450 cytochrome substrates. These experiments suggest that bacterial luciferase is an electron transport chain consisting of several proteins, with cytochrome P-450 as the terminal component.

123. Danilov, V. S. and Yu. A. Malkov (1986). Effect of Heme Ligands of CO and Cyanide on the Reaction Catalyzed by Bacterial Luciferase. *Biochemistry (USSR)* 51(5):782-787 (Russian) :669-673 (English).

The influence of CO on the bioluminescence of the bacteria *Photobacterium fischeri* and *Beneckeia harveyi* and on the activity of luciferase preparations was investigated. Since bacterial luciferase possesses high affinity for oxygen, the experiments were conducted considering the influence of the oxygen content in the medium on the activity of the enzyme. As a result of the experiments it was shown that heme ligands of CO and cyanide inhibit the activity of luciferases, and it is concluded that the CO-binding hemoprotein participates in the reaction of bacterial luminescence.

124. Danilov, V. S., Yu. A. Malkov and N. S. Yegorov (1985). The Effect of CO on the Activity of Bacterial Luciferase. *Stud. Biophys.* 105(3):157-165.

The inhibitory effect of the heme ligand of CO on bioluminescence of bacteria *Photobacterium fischeri* and on purified bacterial luciferase is indicated. The conclusion concerning the functional necessity of the CO-binding hemoprotein (cytochrome P-450) in the light-emitting reaction is made.

125. Daubner, Susan Colette, Adrienne M. Astorga, Gary B. Leisman and Thomas O. Baldwin (1987). Isolation and Characterization of a Yellow Fluorescent Protein from *Vibrio fischeri* Strain Y-1. In *Flavins and Flavoproteins 1987*, D. E. Edmondson and D. B. McCormick, eds., New York: Walter de Gruyter and Co., pp. 637-640.

A decade ago, a yellow light-emitting bacterium, *Vibrio fischeri* strain Y-1, was isolated from seawater off the California coast. This isolate was discovered to possess a bimodal emission spectrum with maxima of 545 nm and 500 nm in vivo. The emission of yellow light, unique to Y-1, was later determined to be due to a secondary emitter, the yellow fluorescent protein (YFP). When added to luciferase in vitro YFP shifts the emission maximum from 485 to 535 nm, with a shoulder at 485 nm. It was also found that the interaction between YFP and luciferase is temperature-sensitive both in vitro and in vivo, and is affected by pH and aldehyde chain length. Here a purification procedure for the yellow fluorescent protein in its active form is presented.

126. Daubner, Susan Colette, Adrienne M. Astorga, Gary B. Leisman and Thomas O. Baldwin (1987). Yellow Light Emission of *Vibrio fischeri* Strain Y-1: Purification and Characterization of the

Energy-accepting Yellow Fluorescent Protein. *Proc. Nat. Acad. US* 84(24):8912-8916.

A strain of luminous bacteria, *Vibrio fischeri* Y-1, emits yellow light rather than the blue-green emission typical of other luminous bacteria. The yellow emission has been postulated previously to result from energy transfer from an electronically excited species formed in the bacterial luciferase-catalyzed reaction to a secondary emitter protein, termed the yellow fluorescent protein (YFP). The purification of YFP to homogeneity without loss of the chromophore is reported. The protein was found to be a homodimer of  $M_r$  22,000 subunits with one weakly bound FMN per subunit. The FMN-protein complex was stabilized by 10% (vol/vol) glycerol in the buffers, allowing purification of the active holo-YFP. The protein migrated as a single spot with an isoelectric point of about 6.5 on two-dimensional polyacrylamide gel electrophoresis and gave an N-terminal sequence of Met-Phe-Lys-Gly-Ile-Val-Glu-Gly-Ile-Ile-Gly-Ile-Glu-Lys-Ile. Addition of purified YFP to a reaction in which luciferase was supplied with FMNH<sub>2</sub> (reduced FMN) by a NADH:FMN oxidoreductase resulted in a dramatic enhancement in the intensity of bioluminescence and an additional peak in the emission spectrum at about 534 nm. The resulting bimodal bioluminescence emission spectrum had peaks at 484 nm, apparently due to emission from the luciferase-flavin complex, and at 534 nm, corresponding to the fluorescence emission maximum of YFP. This bimodal spectrum closely matched the emission spectrum in vivo.

127. Denton, E. J., Peter J. Herring, Edith A. Widder, Michael I. Latz and James F. Case (1985). The Roles of Filters in the Photophores of Oceanic Animals and Their Relation to Vision in the Oceanic Environment. *Proc., R. Soc. London* B225:63-97.

In many of the photophores found in deep-sea fishes and invertebrates, light filters containing pigments lie between the tissues that generate light and the sea. The loss of light within such filters has been measured throughout the visible spectrum for a variety of animals. These filters differ greatly in their spectral absorption characteristics and do not all contain the same pigments. All those from ventral photophores have a transmission band in the blue corresponding to the daylight that penetrates best into oceanic waters. For two fishes it is shown that the light generated inside their photophores is a relatively

poor spectral match for the ambient submarine daylight while the light emitted into the sea, after passing through the filters, is a good match. For a third fish a similar improvement in "color match" is brought about not by passing the light through a filter containing pigments, but by reflecting the light into the sea by a blue mirror. All these observations support the hypothesis that the ventral photophores are used for camouflage. *Malacosteus niger* Ayres 1848 is an oceanic fish which emits red light from a large suborbital photophore. The red light generated inside the photophore is largely absorbed by a colored filter over its external surface which transmits only a band of light of wavelengths around 700 nm. This is a waveband which is heavily absorbed by oceanic seawater. It is shown, however, that animals that can emit and are sensitive to such far-red light will have very great advantages in being able to see without being seen. The ranges over which such red light can be useful for vision are, however, relatively small. The nature of the pigments found in these various photophores is discussed. It is also calculated that the intensities of penetrating daylight are such that visual acuity could be fairly good down to considerable depths in the mesopelagic zone.

128. Dera, Jerzy and Theresa Weglenska (1983). Bioluminescence of Zooplankton in the Antarctic Fiord Ezcurra Inlet. *Oceanologia* 15:185-207.

Zooplankton samples were taken using a 250  $\mu$ -mesh plankton net in the water column from the surface to 70 m (bottom) in Ezcurra Inlet during the Antarctic summer of 1977-1978. Bioluminescent flashing was observed in samples from all depths. The flash intensity ranged from  $10^{-9}$  to  $10^{-5}$   $\mu$ W/cm<sup>2</sup> (at a distance of 20 cm from the source) and duration up to several tens of seconds. Bioluminescence activity was generally greater at "night" (when ambient background light was still too high to permit in situ bathyphotometer measurements) and exhibited three phases: intensive activity associated with shock for 20 to 30 min after capture; a less active stationary phase lasting many hours; and a fading phase in which bioluminescence diminished to near zero for reasons that were not ascertained. The copepod *Metridia* dominated the luminous zooplankton, but euphausiid shrimp also made a major contribution to the light budget. Emission from other unidentified organisms was also observed. The role of bioluminescence was not examined carefully, but mechanically stimuable

bioluminescence seemed to function as a reaction to danger.

129. Donaldson, Thomas Q. (1982). Stimulation of Bioluminescence in *Pyrocystis lunula* and *Gonyaulax polyedra* by Means of Controlled Pressure Changes. MS Thesis, Naval Postgraduate School, Monterey, California.

The threshold pressure change at which stimulated bioluminescence first occurs was measured for the dinoflagellates *Pyrocystis lunula* and *Gonyaulax polyedra*. Cell stimulation was by controlled, repeated, pressure increases and decreases of 1-sec duration. Light was detected by a photomultiplier tube and Argon was used as the pressurizing gas. Experiments were conducted at atmospheric pressure and 30 psi. Further measurements of cell sensitivity as a function of circadian rhythm were also conducted. Stimulation was applied at varying times in the scotophase (dark phase) to determine a peak sensitivity period. Both organisms responded to a pressure decrease with a threshold level of  $3.67 \pm 0.59$  psi/sec for *Pyrocystis lunula* at base pressure. Sensitivity to stimulation was found to be the greatest at the middle of the scotophase, i.e., CT1830.

130. Donaldson, Thomas Q., Stevens P. Tucker and Richard V. Lynch (1983). Stimulation of Bioluminescence in Dinoflagellates by Controlled Pressure Changes. Naval Research Laboratory, Washington, D.C., Report 8772.

Bioluminescence in two species of dinoflagellates, *Pyrocystis lunula* and *Gonyaulax polyedra*, was stimulated when small pressure changes occurred. At an initial pressure of 1 atm, a pressure decrease rate of  $0.25 \pm 0.04$  atm sec<sup>-1</sup> was the mean decrease threshold for *P. lunula*. Small variations in this threshold occurred at a higher initial pressure and at different times during the circadian cycle. Pressure decreases were much more effective than pressure increases. For *G. polyedra*, a pressure change rate of at least  $0.95$  atm sec<sup>-1</sup> was required to stimulate bioluminescence. Pressure increases and decreases were both effective, but decreases were more effective than increases. The variation in results did not lend itself to statistical analysis.

131. Dunlap, Jay C. and J. Woodland Hastings (1981). The Biological Clock in *Gonyaulax* Controls

Luciferase Activity by Regulating Turnover. *J. Biol. Chem.* 256(20):10509-10518.

Luciferase activity in cell-free extracts of the bioluminescent marine dinoflagellate *Gonyaulax polyedra* undergoes a cyclic daily change such that activities of extracts made in the middle of the night phase may be 10 times greater than in extracts of day phase cells. These cyclic changes continue under constant conditions, in a manner indicative of control by an endogenous circadian cellular mechanism. This paper describes the purification and properties of the higher molecular weight unproteolyzed luciferase from both day and night phase cells. Comparisons of the two preparations with respect to several physicochemical, enzymatic and immunological criteria were made in order to establish the basis for the activity difference; no differences between day and night species were found. A given amount of antiluciferase inactivated the same amount of luciferase activity in both day and night extracts; their specific activities are therefore the same. These data strongly suggest that the luciferase is the same polypeptide in day and night extracts and that such extracts contain different amounts of the enzyme. We therefore postulate that the circadian rhythm of luciferase activity is a result of biological clock-controlled synthesis and/or degradation of the luciferase polypeptide.

132. Dunlap, Jay C., J. Woodland Hastings and Osamu Shimomura (1980). Crossreactivity between the Light-Emitting Systems of Distantly Related Organisms: Novel Type of Light-Emitting Compound. *Proc., Nat. Acad. Sci. US* 77(3):1394-1397.

Dinoflagellate luciferin has been found to cross react and emit light with euphausiid photoprotein; and euphausiid fluorescent substance gives luminescence with dinoflagellate luciferase. Luciferin and the fluorescent substance, both highly unstable and fluorescent compounds, are biochemically similar but not identical. Preliminary spectral and chemical data suggest that both compounds contain an open chain polypyrrole structure, novel among compounds so far known to be involved in light emission in any biological system. The dinoflagellates and euphausiids are phylogenetically distant; the possibility that the latter obtain the molecule nutritionally from the former is suggested.

133. Dunlap, Jay C., Walter Taylor and J. Woodland Hastings (1979). Effects of Protein Synthesis and Phosphodiesterase Inhibitors on the Circadian Clock in *Gonyaulax*. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 69.

**ABSTRACT.** Protein synthesis inhibitors strongly phase-shift the circadian clock in *Gonyaulax*. cAMP phosphodiesterase inhibitors do not. These findings implicate protein synthesis in the clock mechanism and cast doubt on the cAMP model for clock function.

134. Dunlap, Jay C., Walter Taylor and J. Woodland Hastings (1980). The Effects of Protein Synthesis Inhibitors on the *Gonyaulax* Clock: Phase-Shifting Effects of Cycloheximide, Puromycin, Emitine, Anisomycin and Streptimidone. *Eur. J. Cell. Biol.* 22 (1):495.

**ABSTRACT.** Cycloheximide phase shifts the circadian glow rhythm of *Gonyaulax polyedra* linearly with the log of the product of pulse strength and duration. Sensitivity to phase-shifting depends on time of day. A point of singularity exists. Anisomycin and streptimidone produce similar effects, but emitine and puromycin result in only small phase shifts.

135. Dunlap, Jay C., Walter Taylor and J. Woodland Hastings (1980). The Effects of Protein Synthesis Inhibitors on the *Gonyaulax* Clock. I. Phase-Shifting Effects of Cycloheximide. *J. Comp. Physiol.* B138:1-8.

Cycloheximide has been shown to be potent in phase-shifting the circadian glow rhythm of the dinoflagellate *Gonyaulax polyedra*. In experiments in which the cells were exposed to drug pulses of varying concentration (0.35  $\mu$ M to 10  $\mu$ M) and duration (0.5 hours to 8 hours), the phase shift produced was linear with the log of the product of pulse strength and duration. The sensitivity to drug-induced phase shifting varies as a function of time of day: both advances and delays occurred and, depending on the strength of the perturbation, resulted in strong or weak-type phase response curves. Pulses given at different times after the light/dark to constant dim transition resulted in a crossover from delays to advances at about 15.5 hours; this crossover point was the same at 19°C and 24°C. The occurrence of extended transients following cycloheximide-induced phase advances (but not delays) appears to be the first

example of such transients in a microbial circadian system.

136. Dunlap, Jay C., Walter Taylor and J. Woodland Hastings (1981). The Control and Expression of Bioluminescence in Dinoflagellates. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis (Minnesota): Burgess Publishing Co., pp. 108-124.

The scintillon model of the bioluminescent flash is presented. This model adequately represents *Gonyaulax polyedra* bioluminescence, but not that of *Pyrocystis* sp., which lack a soluble binding protein. Insufficient data exist to establish conclusively control mechanisms. Dinoflagellate luciferin is identified potentially as a polypyrrole, possibly related to the fluorescence substance from the euphausiid *Meganycitophanes norwegica*.

137. Dunlap, Kathleen and Paul Brehm (1985). Control of Light Emission from Coelenterate Cells Containing Endogenous Calcium-Activated Photoprotein. *Soc. Neurosci. Abstr.* 11(2):1184.

**ABSTRACT.** In the hydrozoan coelenterate *Obelia geniculata* bioluminescence is normally triggered by an action potential which propagates through the non-neural endoderm. Extracellular  $\text{Ca}^{++}$  is required. A transient outward voltage-activated  $\text{K}^+$  current, but not an inward  $\text{Ca}^{++}$  or  $\text{Na}^+$  current, is involved in the stimulation mechanism. It is suggested that activation of the photoprotein through elevation of internal calcium concentration requires interaction with adjacent non-luminescent cells and that this signal occurs by a mechanism other than direct depolarization.

138. Dunlap, Kathleen, K. Takeda and Paul Brehm (1987). Activation of a Calcium-Dependent Photoprotein by Chemical Signalling through Gap Junctions. *Nature* 325:60-72.

In the hydrozoan coelenterate *Obelia geniculata*, epithelial cell action potentials trigger light emission from photocyte effector cells containing obelin, an endogenous calcium-activated photoprotein. As this luminescence is blocked by the removal of extracellular calcium it seemed likely that calcium entry via voltage-gated channels in the photocyte membrane would account for the light emission. However, no inward calcium current was detected in whole cell recordings from dissociated photocytes and

depolarization of isolated photocytes produced no luminescence. In contrast, a voltage-dependent calcium current was recorded from nonluminescent support cells, and activation of this current triggered luminescence in an adjacent photocyte. Surprisingly, light emission was abolished when the gap junctions between the photocyte and support cell were blocked. It is concluded that calcium entry into support cells leads to light emission from neighbouring photocytes via chemical signalling through intercellular gap junctions.

139. Dunlap, Paul V. (1983). Luminescence, Respiration, and Density of *Photobacterium leiognathi* in Light Organs of Leiognathid Fishes: Evidence for Oxygen Competition. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 83:160.

**ABSTRACT.** In vivo specific luminescence of bacterial symbionts from the light organs of leiognathid fishes averaged  $3.8 \times 10^5$  quanta/sec/cell, at least a factor of ten brighter than values for the same bacterium grown in culture. Luminescence accounted for over 50% of the oxygen taken up by the the symbionts. Symbiont density in the light organ tubules was about  $2 \times 10^{10}$  cells/ml. The high density of cells and high proportion of oxygen used in luminescence may result in limiting the in situ growth rate of the symbionts through oxygen competition.

140. Dunlap, Paul V. (1984). Effect of Osmolarity on the Luminescence and Growth of *Photobacterium leiognathi*: A Model of Ponyfish Light Organ Symbiosis. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 84:138.

**ABSTRACT.** Bacterial light organ symbionts of ponyfishes produce much lower light emission under typical culture conditions than in light organs. Low osmolarity, to a level similar to that in light organs, stimulates light emission in cultures to a level equal to that in light organs, and also reduces growth rate. Low osmolarity appears to stimulate autoinducer production and both luciferase synthesis and activity, thus maximizing light production while minimizing the energetic costs of maintaining the symbionts.

141. Dunlap, Paul V. (1984). Physiological and Morphological State of the Symbiotic Bacteria from Light Organs of Ponyfish. *Biol. Bull.* 167(2):410-425.

Symbiotic, bioluminescent bacteria (*Photobacterium leiognathi*) within and directly

removed from the light organs of freshly sacrificed Philippine and Japanese ponyfish (family Leiognathidae) were analyzed for light production, oxygen uptake, morphology and density. Luminescence averaged  $2.4 \times 10^4$  quanta  $\text{sec}^{-1} \text{ cell}^{-1}$  for bacteria from 24 fish (6 species in 3 genera), more than 10 times the maximum luminescences of *P. leiognathi* grown in culture. Light production (depending on the in vivo quantum yield for luminescence, 0.1 to 1.0) accounted for 1.7 to 17% of the total oxygen utilized by bacteria from the light organ, substantially more than found for *P. leiognathi* in culture. Bacteria from the light organ were nonmotile, nonflagellated coccobacilloid to short rod-shaped cells ( $1.6 \times 3.2 \mu\text{m}$ ), whereas in culture they showed motility and polar flagellation. In situ doubling time for the population of light organ bacteria was estimated to be approximately one day, or 20 to 30 times slower than in culture. Within the tubules of the light organ, the bacteria were solidly packed inside elongate, thinly walled saccules, with one to 20 saccules tightly filling each light organ tubule. The saccules held the bacteria at a density (calculated from bacterial cell and saccule volumes) of approximately  $1 \times 10^{11}$  cells  $\text{mL}^{-1}$ , which is a density roughly 15 times greater than estimated from total light organ volume. These findings lead to a maximal-luminescence, minimal-growth bacterial model of this symbiosis.

142. Dunlap, Paul V. (1984). The Ecology and Physiology of the Light Organ Symbiosis between *Photobacterium leiognathi* and Ponyfishes. Ph.D. Dissertation, University of California, Los Angeles.

Using morphological characteristics and characteristics of the light organ, the elongate ponyfish of the Indo-West Pacific Ocean were divided into two species, *Leiognathus elongatus* (Günther) and *L. stercorarius* (Evermann and Seale). The light organ bacteria of *L. elongatus* were successfully cultured for the first time. In the light organ, the bacteria exist at a density of  $10^{11}$  cells/mL, produce  $2.4 \times 10^4$  quanta  $\text{sec}^{-1} \text{ cell}^{-1}$ , and utilize 2 to 20% of the total oxygen taken up. Cultures grown in low osmolarity conditions (400 mOsm, similar to the osmolarity of fish tissue and fluids), produced equal light emission and high luciferase synthesis but low growth and oxygen uptake. Higher osmolarity (800 mOsm, similar to seawater) sharply restricted luminescence but promoted growth and oxygen uptake. Iron limitation

also stimulated luminescence and restricted growth, but less effectively than low osmolarity, which therefore may be a host control factor for the bacterial symbiont. Other species of luminous bacteria responded to low osmolarity in species-specific ways. Ponyfish in general exhibit sexual dimorphism of the light organ system, and *Gazza minuta* produces five different types of displays.

143. Dunlap, Paul V. (1985). Osmotic Control of Luminescence and Growth in *Photobacterium leiognathi* from Ponyfish Light Organs. *Arch. Microbiol.* 141:44-50.

Osmolarity was found to control the luminescence and growth of *Photobacterium leiognathi* strain LN-1a isolated from the light organ of the ponyfish *Leiognathus nuchalis* (family Leiognathidae). Low osmolarity (ca. 400 mOsm) stimulated luminescence per cell 80- to 100-fold to a level (ca.  $2.0 \times 10^4$  quanta  $\text{sec}^{-1} \text{ cell}^{-1}$ ) equal to that of bacteria taken directly from the light organ and increased the level of luciferase per cell 8- to 10-fold compared to high osmolarity (ca. 800 mOsm). Conversely, high osmolarity stimulated oxygen uptake and growth rate 2- to 4-fold compared to low osmolarity. Of 21 additional tested strains of *P. leiognathi* from light organs of nine other ponyfish species, all responded similarly. Low osmolarity may be a host control factor that functions to stimulate the luminescence and restrict the growth of ponyfish light organ bacteria in situ.

144. Dunlap, Paul V., and E. P. Greenberg (1985). Control of *Vibrio fischeri* lux Gene Expression in *Escherichia coli* by cAMP and Catabolite Activator Protein. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 85:144.

**ABSTRACT.** Studies on glucose-repressed mutants of *E. coli* containing cloned *V. fischeri* lux genes showed that cAMP and catabolite activator protein are required for the induction of *V. fischeri* luminescence enzymes in *E. coli*. Since glucose can repress synthesis of these enzymes in *V. fischeri*, an analogous control for lux gene expression in wild strains is postulated.

145. Dunlap, Paul V. and E. P. Greenberg (1985). Control of *Vibrio fischeri* Luminescence Gene Expression in *Escherichia coli* by Cyclic AMP and

Cyclic AMP Receptor Protein. *J. Bacteriol.* 164(1):45-50.

Under certain conditions glucose represses the autoinducible synthesis of luminescence enzymes in *Vibrio fischeri*. To examine the genetic regulation of luminescence more closely, *Escherichia coli* catabolite repression mutants were transformed with a plasmid (pJE202) that contains *V. fischeri* genes specifying the luminescence enzymes and encoding regulatory functions for luminescence (the *lux* genes) or with plasmids (pJE413 and pJE455) containing transcriptional fusions between the *lacZ* gene on transposon mini-Mu and specific genes in each of the two *lux* operons. Unless cyclic AMP (cAMP) was added to the growth medium, an adenylate cyclase deletion mutant containing pJE202 produced very little light and low levels of the light-emitting enzyme luciferase. A mutant that does not make cAMP but does make an altered CRP which does not require cAMP for activity produced induced levels of luminescence after transformation with pJE202. To test the effects of cAMP and CRP on each of the two *lux* operons separately rather than on both together, the *E. coli* catabolite repression mutants were transformed with pJE413 and pJE455. From measurements of  $\beta$ -galactosidase and luciferase activities it appeared that cAMP and CRP affected transcription of both *lux* operons. In the presence of autoinducer and its receptor, transcription of the operon encoding all the luminescence genes except the receptor gene appeared to be activated by cAMP and CRP, whereas in the absence of the receptor, cAMP and CRP appeared to decrease transcription of this operon. Transcription of the operon encoding the autoinducer receptor appeared to be stimulated by cAMP and CRP in the absence of the receptor itself. These results demonstrate that cAMP and CRP are required for proper control of the *V. fischeri* luminescence system and suggest that *lux* gene transcription is regulated by a complex mechanism.

146. Dunlap, Paul V. and E. P. Greenberg (1987). Analysis of the Mechanism of *Vibrio fischeri* Luminescence Gene Regulation by cAMP and cAMP Receptor Protein in *Escherichia coli*. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 87:169.

**ABSTRACT.** Studies on genetically modified *E. coli* containing *V. harveyi lux* genes showed that in the presence of high levels of *lux* receptor protein, cAMP

and cAMP receptor protein are not required for induction of luminescence.

147. Dunlap, Paul V. and Margaret J. McFall-Ngai (1984). *Leiognathus elongatus* (Perciformes:Leiognathidae): Two Distinct Species Based on Morphological and Light Organ Characters. *Copeia* 1984(4):884-892.

The morphological description of the bacterially bioluminescent elongate leiognathid, *Leiognathus elongatus*, unites those ponyfishes having cheek scales and a standard length of 0.33 or less in body depth. This report reassesses the taxonomic status of fish identified as *L. elongatus* by these criteria using specimens obtained in the Philippine Islands and Japan in 1982 and 1983. Based on differences in external morphology and components of the internal light-organ system, the specimens fall into two distinct groups (I and II). Group I fish are 20% deeper bodied, have 30% more lateral line scales and a more finely detailed dorso-lateral mottling pattern than group II specimens. Differences in the supraorbital spine, posterior margin of the adipose eyelid and snout pigmentation further distinguish these fishes. Additionally, group I fish exhibit a less pronounced sexual dimorphism; males have a sex-specific blue lateral stripe and a light organ two to three times larger in volume than that of females. In contrast, group II fish are distinctly dimorphic, with males differing from females in three morphological features of the light-organ system: a sex-specific clear flank patch, transparent lateral gas bladder walls and a greatly enlarged light organ (20 to 100 times larger than that of females). Based on these differences and on comparisons with type specimens, two species were recognized: *L. stercorarius* Evermann and Seale (group I), a previously buried synonym of *L. elongatus*; and *L. elongatus* (Günther) (group II), which includes fishes previously named *Equula elongata* (Günther), *L. elongatus* (Smith and Pope) and *L. popei* (Whitley). The use of the light-organ system in clarifying questions of leiognathid taxonomy is proposed.

148. Dunlap, Paul V. and Margaret J. McFall-Ngai (1987). Initiation and Control of the Bioluminescent Symbiosis between *Photobacterium leiognathi* and Leiognathid Fish. *Ann. N. Y. Acad. Sci.* 503 (Endocytobiology III):269-283.

The morphologies of the ponyfish light organ and its bacterial symbiont *Photobacterium leiognathi* are described. Types of luminescent displays and their probable functions are tabulated. A physiological mechanism for control of light emission through the storage and release of oxygen from the gas bladder is postulated. It is further suggested that low osmolarity is a host control factor for restricting growth and stimulating luminescence of *P. leiognathi* in the light organ. The possibility of iron limitation as a host control mechanism is also discussed.

149. Dupaix, Alain, Bernard Arrio, Bernard Lécuyer, Chantal Fresneau, Pierre Volfin, Jean-Claude Merlin, Paul Dhamelincourt and Bertin De Bettignies (1982). Intracellular Spectroscopic Studies of a Bioluminescent Cell: *Pyrocystis lunula*. *Biol. Cell.* 43:157-162.

Until now, the location of the light emitting reaction in dinoflagellate algae like *Noctiluca miliaris*, *Gonyaulax polyedra* and *Pyrocystis lunula* has been the object of conflicting reports. The existence of organelles, which would be the light emission centers, has not been unambiguously proved, either by electron microscopy in integral cells or in subcellular fractions obtained by zonal centrifugation. Therefore, scanning and mapping techniques should be of particular interest in obtaining some information about location of intracellular components and enzymatic reactions. Photon counting techniques, associated with image intensifiers, are sensitive enough to locate light sources as small as 1  $\mu$ m diameter and to provide fluorescence and Raman spectra. The first results obtained in this field with the laser Raman molecular microprobe (M.O.L.E.) on *Pyrocystis lunula* are presented.

150. Dupaix, Alain, Chantal Fresneau, Pierre Volfin, Bernard Arrio and Bernard Lécuyer (1981). Biochemical Studies of the Bioluminescent Polynoid Worms. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, p. 525.

**ABSTRACT.** Chromatography of the homogenate of the elytra of polynoid worms using A6 Ultragel led to two main peaks, one excluded in the void volume and the other in the total volume of the column. Kinetic studies of the luminous reaction in the presence of different triggering agents suggested

a peroxidasic-like mechanism for the bioluminescent reaction.

151. Dzhunkovskaya, I. P., V. I. Sukharevich, V. E. Shkinke and Z. A. Viesture (1985). Effect of Kerogen Oxidation Products on Growth and Luminescence in *Photobacterium fischeri*. *Microbiol. (USSR)* 54(1):89-92 (Russian) :75-78 (English).

The effect of oxidation of shale kerogen (high-molecular-weight acids, HMA) on the growth and luminescence of bacteria was studied. HMA did not affect the increase in biomass, reduced cell luminescence and increased luciferase synthesis appreciably. HMA bonded directly to luciferase and altered the ratio of NADH-FMN oxidoreductase and luciferase activities in cells. It is suggested that HMA act as inhibitors of oxidases with mixed functions.

152. Eberhard, Anatol, A. L. Burlingame, C. Eberhard, G. L. Kenyon, Kenneth H. Nealson, and N. J. Oppenheimer (1981). Structural Identification of Autoinducer of *Photobacterium fischeri* Luciferase. *Biochemistry* 20(9):2444-2449.

Synthesis of bacterial luciferase in some strains of luminous bacteria requires a threshold concentration of an autoinducer synthesized by the bacteria and excreted into the medium. Autoinducer excreted by *Photobacterium fischeri* strain MJ-1 was isolated from the cell-free medium by extraction with ethyl acetate, evaporation of solvent, workup with ethanol-water mixtures, and silica gel chromatography, followed by normal-phase and then reverse-phase high-performance liquid chromatography. The final product was >99% pure. The structure of the autoinducer as determined by high-resolution  $^1\text{H}$  nuclear magnetic resonance spectroscopy, infrared spectroscopy, and high-resolution mass spectrometry was N-(3-oxohexanoyl) 3-aminodihydro-2( $^3\text{H}$ )-furanone [or N-( $\beta$ -ketocaproyl) homoserine lactone]. The formation of homoserine by hydrolysis of the autoinducer was consistent with this structure. Synthetic autoinducer, obtained as a racemate, was prepared by coupling homoserine lactone to the ethylene glycol ketal of sodium 3-oxohexanoate, followed by mildly acidic removal of the protecting group; this synthetic material showed the appropriate biological activity.

153. Eberhard, Anatol, A. Burlingame, C. Eberhard, G. L. Kenyon and N. J. Oppenheimer (1980). Isolation and Identification of the Autoinducer of

*Photobacterium fischeri* Luciferase. Abstr., Ann. Meet. Amer. Soc. Microbiol. 80:154.

**ABSTRACT.** The autoinducer of luciferase synthesis in *Photobacterium fischeri* is stable to heat, acid, mild oxidation and mild reduction, but very sensitive to base. It is non-ionic and has both polar and nonpolar groups. Its structure has been determined to be N-(3-oxohexanoyl)-3-aminodihydro-2(3H)-furanone.

154. Eberhard, Anatol, C. Eberhard, A. L. Burlingame, G. L. Kenyon, N. J. Oppenheimer and Kenneth H. Nealson (1981). Purification, Identification and Synthesis of *Photobacterium fischeri* Autoinducer. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 113-120.

The methods of assaying, purifying and synthesizing autoinducer from *P. fischeri* are given in schematic form. Identification procedures are outlined and the structure is depicted. Identity of the synthesized autoinducer with the natural material is confirmed.

155. Eberhard, Anatol, Johanna P. Hinton and Robin M. Zuck (1979). Luminous Bacteria Synthesize Luciferase Anaerobically. *Arch. Microbiol.* 121:277-282.

Four species of luminous bacteria, *Photobacterium phosphoreum*, *P. leiognathi*, *P. fischeri* and *Beneckea harveyi* (two strains of each), were shown to synthesize luciferase anaerobically. One of these, *P. phosphoreum*, produced as much luciferase anaerobically as it did aerobically and all four species were found to grow almost equally rapidly under the two sets of conditions. Previous work with *B. harveyi* and *P. fischeri* had shown that aerobic luciferase synthesis can proceed only after an inhibitor in the complex medium has been removed and a species-specific autoinducer secreted. All strains tested also removed the inhibitor and secreted an autoinducer anaerobically. The small amount of luciferase produced anaerobically by some strains is thus apparently not due either to lack of removal of inhibitor or to insufficient production of autoinducer but may involve an oxygen-dependent control mechanism.

156. Eberhard, Anatol, Cindra A. Widrig, Paula McBath and Jeffrey B. Schineller (1986). Analogs of the Autoinducer of Bioluminescence in *Vibrio fischeri*. *Arch. Microbiol.* 146:35-40.

The enzymes for luminescence in *Vibrio fischeri* are induced only when a sufficient concentration of a metabolic product (autoinducer) specifically produced by this species accumulates. It has previously been shown that the autoinducer is 3-oxohexanoyl homoserine lactone and that it enters the cells by simple diffusion. To further study the mechanism of induction, several analogs of the autoinducer were synthesized. The analogs were tested with *V. fischeri* for their inducing activity and for their ability to inhibit the action of the natural autoinducer. The compounds were found to display various combinations of inducing and inhibiting abilities. None of the compounds tested appeared to have any effect on cells of *V. harveyi* strain MAV or *Photobacterium leiognathi* strain 721, but several of the compounds decreased light output by *P. phosphoreum* strain 8265. These studies show that (1) the site of action of the autoinducer is not highly sterically constrained (2) the autoinducers of other species of luminous bacteria are likely to be quite different from that of *V. fischeri* and (3) a simple mode in which one autoinducer molecule binds to a single receptor protein site and thus initiates luciferase synthesis is inadequate. The analogs should prove useful in the study of the binding site and mode of action of the autoinducer.

157. Eley, Michael H. (1982). Physiology and Biochemistry of Bioluminescent Marine Bacteria. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 195-212.

*Photobacterium phosphoreum* emitted the maximum amount of light at a pH between 6.0 and 6.5, temperature of 15°C, and in a medium containing yeast extract. The increased emission was due to higher luciferase content. Quantum yields and kinetic properties of luciferase with various aldehydes were reported.

158. Emson, R. H. and Peter J. Herring (1985). Bioluminescence in Deep and Shallow Water Brittlestars. *Proc., Int. Echinoderm Conf.* 5:656.

Bioluminescence in *Amphiura filiformis* and *Acrocnida brachiata* is confined to the arm spines and the light sources do not fluoresce. In all other

species luminescence is widespread in the arms but is concentrated in certain regions such as the area of the arm spine nerve ganglia and the light sources fluoresce. In *A. filiformis* the light sources appear to be the basophilic gland cells, which contain densely staining spherical granular bodies. These structures are lacking in *Ophiacantha abyssicola*, *Ophiopsila riisei*, and *A. grandisquama*. These contain instead cells with secretions of finely granular material, which are suggested to be the sources of light. The abundance of both types of light-emitting cells suggests that luminescence is important in the life of these brittlestars or that the luminescent cells have multiple functions.

159. Engebrecht, JoAnne, Kenneth H. Nealson and Michael R. Silverman (1983). Regulation of Bacterial Bioluminescence. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 83:121.

**ABSTRACT.** Studies on *Escherichia coli* containing cloned *V. fischeri lux* genes showed that synthesis of autoinducer and response to autoinducer are controlled by two *lux* gene operons. Expression of one of these operons is dependent on the presence of autoinducer.

160. Engebrecht, JoAnne, Kenneth H. Nealson and Michael R. Silverman (1983). Bacterial Bioluminescence: Isolation and Genetic Analysis of Functions from *Vibrio fischeri*. *Cell* 32:773-781.

Recombinant *E. coli* that produce light were found in a clone library of hybrid plasmids containing DNA from the marine bacterium *Vibrio fischeri*. All luminescent clones had a 16-kb insert that encoded enzymatic activities for the light reaction, as well as regulatory functions necessary for expression of the luminescence phenotype (*Lux*). Mutants generated by transposons Tn5 and mini-Mu were used to define *Lux* functions and to determine the genetic organization of the *lux* region. Regulatory and enzymatic functions were assigned to regions of *lux* operons. With transcriptional fusions between the *lacZ* gene on transposon mini-Mu and the target gene, expression of *lux* operons could be measured in the absence of light production. The direction of transcription of *lux* operons was deduced from the orientation of mini-Mu insertions in the fusion plasmids. Induction of transcription of one *lux* operon required a function encoded by that operon (autoregulation). From these

and other regulatory relationships, a model for genetic control of light production is proposed.

161. Engebrecht, JoAnne and Michael R. Silverman (1984). Identification of Genes and Gene Products Necessary for Bacterial Bioluminescence. *Proc., Nat. Acad. Sci. US* 81:4154-4158.

Expression of luminescence in *Escherichia coli* was recently achieved by cloning genes from the marine bacterium *Vibrio fischeri*. One DNA fragment on a hybrid plasmid encoded regulatory functions and enzymatic activities necessary for light production. The results of a genetic analysis to identify the luminescence genes (*lux*) that reside on this recombinant plasmid are reported. The *lux* gene mutations were generated by hydroxylamine treatment, and these mutations were ordered on a linear map by complementation in *trans* with a series of polar transposon insertions on other plasmids. The *lux* genes were defined by complementation of *lux* gene defects on pairs of plasmids in *trans* in *E. coli*. Hybrid plasmids were also used to direct the synthesis of polypeptides in the *E. coli* minicell system. Seven *lux* genes and the corresponding gene products were identified from the complementation analysis and the minicell programming experiments. These genes, in the order of their position on a linear map, and the apparent molecular weights of the gene products are *luxR* (27,000), *LuxI* (25,000), *luxC* (53,000), *luxD* (33,000), *luxA* (40,000), *luxB* (38,000), and *luxE* (42,000). From the luminescence phenotypes of *E. coli* containing mutant plasmids, functions were assigned to these genes: *lux4A*, *luxB*, *luxC*, *luxD*, and *luxE* encode enzymes for light production and *luxR* and *luxI* encode regulatory functions.

162. Engebrecht, JoAnne and Michael Silverman (1987). Nucleotide Sequence of the Regulatory Locus Controlling Expression of Bacterial Genes for Bioluminescence. *Nucleic Acids Res.* 15(24):10455-10467.

Production of light by the marine bacterium *Vibrio fischeri* and by recombinant hosts containing cloned *lux* genes is controlled by the density of the culture. Density-dependent regulation of *lux* gene expression has been shown to require a locus consisting of the *luxR* and the *luxI* genes and two closely linked divergent promoters. As part of a genetic analysis to understand the regulation of the bioluminescence, the region of DNA containing this

control circuit are sequenced. Open reading frames corresponding to *luxR* and *luxI* were identified; transcription start sites were defined by S1 nuclease mapping and sequences resembling promoter elements were located.

163. Engebrecht, JoAnne, Melvin I. Simon and Michael R. Silverman (1985). Measuring Gene Expression with Light. *Science* 227:1345-1347.

Light is produced by recombinant *Escherichia coli* that contain *lux* genes cloned from the marine bacterium *Vibrio fischeri*. The bioluminescence phenotype requires genes for regulatory and biochemical functions, the latter encoded by five *lux* genes contained in a single operon. These *lux* genes were disconnected from their native promoter and inserted into the transposon mini- $\mu$ . The resulting transposon, mini- $\mu$  *lux*, could induce mutations by insertional inactivation of a target gene, and the *lux* DNA was oriented to align target gene transcription with that of the *lux* genes. Genes in *E. coli* and *Vibrio parahaemolyticus* were mutagenized, and mutants containing transposon-generated *lux* gene fusions produced light as a function of target gene transcription. Light production offers a simple, sensitive, in vivo indicator of gene expression.

164. Evstigneev, P. V. (1982). Changes in Characteristics of Bioluminescent Signals during Ontogenesis of Copepods of the Genus *Pleuromamma*. *Biol. Morya* 8(5):55-59 (Russian); 281-284 (English).

The results of measuring the characteristics of bioluminescence of different age stages of copepods *Pleuromamma piseki* and *P. gracilis*, obtained from plankton and in monocultures, were analyzed. It was shown that the emission of light from organisms in different stages of ontogenesis differed. The increase of energy capacity of light radiation in ontogenesis is associated with the growth of organisms. The ability to emit light appears on the fourth to fifth day of development and is characteristic for the late naupliar and subsequent age stages. Statistically reliable differences in bioluminescence between males and females, as well as between the investigated species, were determined.

165. Evstigneev, P. V. (1983). Bioluminescence of *Pleuromamma piseki* under Electric Stimulation. *Ekol. Morya* 14:52-56 (Russian).

Light response characteristics have been studied in *Pleuromamma piseki*, one of the abundant copepod species of the Indian Ocean. Differences in the level of emitted light energy have been revealed for males and females, for different age stages as well. Bioluminescent responses of one and the same organism are found to be different depending on the type of stimulation.

166. Evstigneev, P. V. (1984). Formation of the Reaction of Radiation of Light during Individual Development of Copepods of the Genus *Pleuromamma*. In *Proc., Third All-Union Conf. on Animal Behavior*, Vol. 1. *Behavioral Mechanisms*, A. A. Zakharov, ed., Izdatel'stvo Nauka, Moscow, pp. 96-97.

This paper was not available for review.

167. Evstigneev, P. V. (1984). Ecological Aspects of the Bioluminescence of Sea Copepods. In *Proc., Third All-Union Conf. on Animal Behavior*, Vol. 2. *Behavior of Animals in Communities*, A. A. Zakharov, ed., Moscow: Izdatel'stvo Nauka, p. 44.

This paper was not available for review.

168. Evstigneev, P. V. (1986). Luminescence of Copepods under Stimulation of Various Types. *Ekol. Morya Akad. Nauk Ukr. SSR* 22:70-75 (Russian).

Statistically significant differences are shown in the characteristics of bioluminescence signals evoked by various types of stimulation. The maximal values of the time and energy parameters of luminescence of copepods from the *Pleuromamma* genus are observed under chemical stimulation. The mechanical excitation induces an order-lower intensity flashes. There are differences in the flash kinetics as well: less synchronous outburst of the light substrate is observed under chemical stimulation than in the case of mechanical and electrical excitations. Duration of the stimulus effect is the most essential characteristic of the irritant affecting all the parameters of the light signal.

169. Feldman, Kathleen A. and John D. Buck (1984). Distribution and Characterization of Luminescent Bacteria in a Temperate Estuary. *Estuaries* 7(1):93-97.

The effect of temperature and salinity on numbers of luminescent bacteria present in waters of the Mystic (Conn.) River estuary was evaluated. Counts decreased with decreasing salinity; none were

detected at freshwater stations. A population maximum of 35 per mL was noted at the highest salinity station ( $30 \pm 2\%$ ). Highest counts were observed during winter and spring and lowest numbers occurred during summer and fall months. Isolates (111) were identified and compared with previously-described luminescent bacteria; i.e., *Beneckea* (*Vibrio*) *harveyi*, *Photobacterium* (V.) *fischeri*, *P. phosphoreum* and *P. leiognathi*. All species were isolated but distinct seasonal differences were noted. *P.* (V.) *fischeri* and *B.* (V.) *harveyi* represented 93% of the luminous population on an annual basis. Only the former was found during the period December through March (highest count 7 per mL), while *B.* (V.) *harveyi* was the dominant species noted between May and October (maximum count 11 per mL). *P. leiognathi* and *P. phosphoreum* were found only during July and August as 7% of the total luminous population. All isolates grew at NaCl concentrations between 6 and 30‰; none grew below 6‰.

170. Filimonov, V. S. and G. M. Sadovskaya (1981). Bioluminescence of Heterogenous Populations of Luminescent Species of Phytoplankton during Ultrasound Stimulation. *Biol. Morya* 8(2):51-57 (Russian) :99-104 (English).

Methods of quantitative assessment of bioluminescence of a heterogenous population of plankton by three parameters—intensity, energy and decrement of luminescence—are presented. The dependence of bioluminescence on abundance of Dinophyta and intensity of stimulation is shown.

171. Filimonov, V. S. and G. M. Sadovskaya (1986). Photoinhibition of Phytoplankton Bioluminescence. *Oceanology* (USSR) 26(5):821-823 (Russian) :621-622 (English).

Experimental data on the rate of photoinhibition of bioluminescing dinoflagellates in plankton samples demonstrate that for white light it depends on illumination level and is practically independent of the species makeup of the phytoplankton community.

172. Filimonov, V. S. and N. A. Tyul'kova (1981). Characteristics of Bioluminescent Impulses of Single Cells of Dinoflagellates. *Biol. Morya* 7(3):43-49 (Russian) :188-193 (English).

The dependences of amplitudes, durations, durations of front edges and latent periods of bioluminescent impulses of the cells of some species

of dinoflagellates on parameters of mechanical and ultrasonic stimuli are discussed. Analysis of the amplitudes and type of responses by both means of stimulation suggests that their effect on the cell is identical. Average values of amplitudes and duration of bioluminescent impulses are typical values for the species, while latent periods and duration of leading edges are the same for all the investigated species.

173. Filimonov, V. S., N. A. Tyul'kova and G. M. Sadovskaya (1982). Luminescence of Dinoflagellates by Ultrasonic Stimulation. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 165-177.

Bioluminescence is stimulated in dinoflagellates of the genera *Peridinium* and *Pyrophacus* by ultrasonic stimuli. A dependence on the intensity and duration of the stimulus is noted. The threshold sensitivity for stimuli of long duration is  $0.02-0.06 \text{ W/cm}^2$ . A gradual dependence of flash duration and amplitude on intensity and duration of the stimulus is reported for some species but not others. However, the duration and kinetics of the flash response in all species tested do depend on stimulus parameters. The response saturates at a stimulus of 10 to 20 msec duration. Exhaustion occurs if the interval between stimuli is less than 5-10 min, with the rate of exhaustion increasing as the interval decreases. The latency period between stimulus and response increases as stimulus intensity decreases. Ultrasonic stimulation also elicits a bioluminescent response from sea samples containing mixed populations of organisms, but the organisms cannot be identified from their responses.

174. Fisher, Arthur (1983). Bioluminescence. *Pop. Sci.* 223(2):8.

At the American Chemical Society meeting in March, 1982, Jon Losee of the Naval Ocean Systems Center in San Diego reported mapping bioluminescence from St. Croix to the Arctic Ocean and correlating it with biomass abundance, thermal gradients and depth. It was suggested that bioluminescence could be used as an index of surface mixing or layer turbulence and to detect thermal fronts.

175. Fredriksson, G. and R. Olsson (1981). The Oral Gland Cells of *Oikopleura dioica* (Tunicata

Appendicularia). *Acta Zool.* (Stockholm) 62(3):195-200.

Light and electron microscopic studies showed that the oral gland cells have two quite different zones. Medially, the basal zone is in contact with body fluids and the endostyle. Its strongly pyroninophile cytoplasm contains the extremely digitated nucleus and numerous small mitochondria. Laterally, the apical zone contacts the epidermis and it may also send a process between epidermal cells and deliver cell fragments into the primordium of the new house. This cell zone contains numerous membranes. It is concluded that the oral gland cells are light producing glands and that the membrane-rich cell fragments which are incorporated into the house wall are the source of the bioluminescence which has been reported from empty houses. The ontogenetically related subchordal cells have a similar structure and it is possible that also these cells are light producers.

176. Freeman, Gary (1987). Localization of Bioluminescence in the Siphonophore *Nanomia cara*. *Mar. Biol.* 93:535-541.

The base of the tentacle of the developing physonect larva (*Nanomia cara*) has a bioluminescent region. The ability to produce light in the larva is transitory: this ability first appears at about 2 days of development and is disappearing by 8 days, as the larva begins to feed. Subsequently paired, bilaterally symmetrical bioluminescent organs are found on the nectophores and the bracts of the adult colony. In both the larva and the adult, bioluminescence is mediated by a calcium specific photoprotein. In all cases the photocytes lack a green fluorescent protein.

177. Fresneau, Chantal, Bernard Arrio, A. Binet, Alain Dupaix, Bernard Lécuyer and Pierre Volfin (1979). Purification and Properties of the Dinoflagellate Luciferin Isolated from *Pyrocystis lunula*. In *Proc., Int. Symp. on Analytical Applications of Bioluminescence and Chemiluminescence*, E. Schram and P. Stanley, eds., Westlake Village (California): State Printing and Publishing, Inc., pp. 620-636.

The purification of the luciferin, isolated from *Pyrocystis lunula*, has been carried out by means of gel chromatography. Chromatographies were performed on Sephadex LH 20 in water at 4°C. The degree of purity was checked by high voltage paper electrophoresis at pH 5.9. The apparent molecular

weight was estimated to 500 daltons by gel chromatography. The absorption spectrum of luciferin shows two maxima centered at 390 and 250 nm, respectively. Luciferin is a fluorescent molecule emitting at 480 nm when excited at 390 nm. The fluorescence emission spectrum is rigorously identical to the in vitro bioluminescence spectrum. In the presence of luciferase, the fluorescence intensity of the substrate decreases at the same rate as the bioluminescence intensity. An apparent isoelectric point equal to 3 has been observed by electrofocusing. Luciferin is able to reduce cytochrome c: this property allows titration of luciferin.

178. Fresneau, Chantal, M. Hill, Nicole Lescure, Bernard Arrio, Alain Dupaix and Pierre Volfin (1986). Dinoflagellate Luminescence: Purification of a NAD(P)H-Dependent Reductase and of Its Substrate. *Arch. Biochem. Biophys.* 251(2):495-503.

The soluble enzymatic luminescent system of the dinoflagellate *Pyrocystis lunula* (luciferase-luciferin) is coupled with an enzymatic NAD(P)H-dependent reaction. The enzyme is a soluble reductase (M<sub>r</sub> 47,000) which catalyzes, in the presence of NAD(P)H, the reduction of a molecule called P630. Reduced P630 has the same spectral characteristics as the purified luciferin. The luciferase can oxidize this reduced molecule with a light emission at 480 nm. These observations suggest that reduced P630 is a luciferin molecule. The oxidized form seems, in these conditions, to be the precursor of luciferin.

179. Friedrich, W. F. and E. P. Greenberg (1983). Glucose Repression of Luminescence and Luciferase in *Vibrio fischeri*. *Arch. Microbiol.* 134:87-91.

The autoinduction and glucose repression of luciferase synthesis in batch cultures and continuous cultures of *Vibrio fischeri* were investigated. As previously reported, a lag in luciferase synthesis occurred in glycerol-grown batch cultures and addition of D-glucose to the medium extended the lag period. A phosphate-limited chemostat culture with D-glucose as energy source (specific growth rate,  $\mu = 0.45 \text{ h}^{-1}$ ) contained uninduced levels of luciferase. Luciferase activity increased to an induced level upon addition of cAMP or autoinducer to such a chemostat culture while cell mass remained constant. Furthermore, when  $\mu$  of a phosphate-limited chemostat culture containing D-glucose as energy source was decreased from 0.45 to  $0.30 \text{ h}^{-1}$ , luciferase activity increased from an

uninduced to induced level. After exogenously added cAMP or autoinducer was diluted out of a phosphate-limited continuous culture or after  $\mu$  was increased to  $0.45 \text{ h}^{-1}$ , luciferase activity remained at an induced level. Apparently, luciferase in *V. fischeri* was subject to a catabolite repression by D-glucose that could be overridden by autoinduction or by an autogenous control element.

180. Fukasawa, Shigeki and Paul V. Dunlap (1986). Identification of Luminous Bacteria Isolated from the Light Organ of the Squid, *Doryteuthis kensaki*. *Agric. Biol. Chem.* 50(6):1645-1646.

The luminous bacterial symbionts isolated from the light organs of the squid *Doryteuthis kensaki*, collected in January 1984 off the coast of Kochi prefecture, Japan, are identified as *Photobacterium leiognathi*.

181. Galt, Charles P. (1980). Distribution of Bioluminescence among Larvacean Tunicates. *Amer. Zool.* 20(4):851.

**ABSTRACT.** Mechanically stimulated luminescence from small, fluorescent granules in the rudimentary houses has previously been reported for four species of *Oikopleura*. Early authors also implicated the oral glands in light production. Recent studies have shown that luminescence also occurs in *Oikopleura rufescens*, *Stegosoma magnum* and *Megalocercus huxleyi*, none of which possesses house fluorescent granules and the last of which lacks oral glands. These results indicate widespread bioluminescence among the Oikopleuridae and the existence of a second method for light production.

182. Galt, Charles P. (1986). Bioluminescence in the Sea: Overview and Current Research. In *Souvenir Program of the International Conference on Marine Science of the Arabian Sea*, March 29-April 2, 1986. Institute of Marine Sciences, University of Karachi, Karachi, Pakistan, pp. 52-53.

This abstract summarizes key research issues of current naval interest and describes preliminary results of a cruise sponsored by the Naval Oceanographic Office and Office of Naval Research in the western Indian Ocean and Arabian Sea. Recommendations for future research in the area are made.

183. Galt, Charles P. and Matthew S. Grober (1985). Total Stimulable Luminescence of *Oikopleura* Houses (Urochordata, Larvacea). *Bull. Mar. Sci.* 37(2):765.

**ABSTRACT.** Mechanical stimulation of discarded *Oikopleura* houses produced an average total integrated light emission (TSL) of  $0.5 \times 10^{12}$  quanta/house, with a maximum of  $2 \times 10^{12}$  quanta/house. Peak flash intensities ranged up to  $1.5 \times 10^{12}$  quanta/sec. TSL increased with animal size and number of luminous inclusions per house and decreased with age, reaching zero in two days. TSL per luminous inclusion is  $10^8$  to  $10^9$  quanta, similar to the values for individual dinoflagellate cells.

184. Galt, Charles P., Matthew S. Grober and Paul F. Sykes (1985). Taxonomic Correlates of Bioluminescence among Appendicularians (Urochordata: Larvacea). *Biol. Bull.* 168(1):125-134.

Larvaceans, common members of marine plankton communities, filter-feed with renewable, external, mucous houses. The houses of some species of Oikopleuridae produce endogenous bioluminescent flashes upon mechanical stimulation and may contribute significantly to surface luminescence. To determine which members of the Oikopleuridae are luminescent, several species were examined for stimulable luminescence and for morphological features responsible for or associated with light production. Luminescence is newly reported from house rudiments and from clean particle-free houses of *Oikopleura rufescens* and *Stegosoma magnum*. In these species, light emanates from previously undescribed fluorescent inclusions in the house rudiment. Neither fluorescence nor luminescence was detected from other parts of the body. Both species also possess oral glands, which apparently are not directly involved in light production but serve as a convenient taxonomic marker of luminescence. All six known luminescent species of larvaceans possess fluorescent and luminescent house rudiment inclusions and oral glands. They predict on these morphological grounds that all 12 species of *Oikopleura* (*Vexillaria*) plus the oikopleurids *S. magnum* and *Folia gracilis* are luminescent. In two other oikopleurids that lack oral glands, *O. fusiformis* and *Megalocercus huxleyi*, neither fluorescent inclusions nor luminescence were detected in clean houses and animals with house rudiments. However, some field-collected houses of these species produced luminescent flashes, perhaps from dinoflagellates on or in the houses. This report

should facilitate assessment of the contribution of larvaceans to surface luminescence on a global scale.

185. Galt, Charles P. and Paul F. Sykes (1983). Sites of Bioluminescence in the Appendicularian *Oikopleura dioica* and *O. labradoriensis* (Urochordata: Larvacea). *Mar. Biol.* 77:155-159.

Although bioluminescence is known in larvacean tunicates, its origin has not been reported. Two species, *Oikopleura dioica* and *O. labradoriensis*, from the northeastern Pacific Ocean, were examined during 1979-1982 to determine the sites of luminescence. An appendicularian lives within a secreted, mucous house and its body is tightly invested by a house rudiment. Mechanical stimulation elicited multiple, summated blue-green flashes from free individuals invested by house rudiments and from empty houses that were virtually free of contamination by exogenous luminescent bacteria or dinoflagellates. Direct microscopic observations showed that the light is produced by clusters of 1 to 2  $\mu\text{m}$  fluorescent granules that form intricate, species-specific patterns of inclusions in the house rudiment. These granular inclusions are probably present in the expanded house, where they account for the multiple, point-sources of light observed in flashing houses. Neither fluorescence nor luminescence was observed in any other parts of the house rudiments, expanded houses, or free appendicularians (including the oral glands, which were previously suspected of producing bioluminescent secretions).

186. Gariépy, Pierre and Michel Anctil (1983). A Pharmacological Study of Adrenergic and Serotonergic Mechanisms in the Photophores of the Midshipman Fish, *Porichthys notatus*. *Comp. Biochem. Physiol.* 74C:341-347.

The effects of adrenergic and serotonergic drugs on luminescence induced by electrical stimulation, adrenaline and noradrenaline were investigated from isolated strips of skin photophores of *Porichthys notatus*. The luminescent response to repeated exposure to adrenaline or noradrenaline displayed concentration-dependent changes in amplitude, higher doses resulting in a drop and lower doses in an increase of amplitude of responses elicited after the initial response. Phenylephrine induced luminescence at a low concentration (100 nM), whereas isoproterenol was ineffective. The alpha (phentolamine, yohimbine) and beta antagonists

(metoprolol, propranolol) all suppressed to a large extent luminescent responses to electrical and catecholamine stimulation. Serotonin (5-HT, 1 to 10  $\mu\text{M}$ ) suppressed nonfacilitated luminescent responses to electrical stimulation, but failed to influence the facilitated responses. Also, 5-HT reduced the luminescent responses to consecutive adrenaline challenges in a concentration-dependent manner. Methysergide (10  $\mu\text{M}$ ) antagonized the inhibitory action of 5-HT on, and potentiated responses to, electrical stimulation. It was ineffective on adrenaline-induced responses. The results suggest that alpha adrenoceptors are the principal receptor type mediating luminescence excitation in *Porichthys photophores*. An inhibitory presynaptic role is postulated for 5-HT, although a postsynaptic mechanism may also be present.

187. Garrod, Christopher K., L. A. Frank and J. D. Craven (1981). The First Search for Marine Bioluminescence from a Spacecraft Using the DE Imaging Instrumentation. *EOS* 62(45):996.

**ABSTRACT.** A search for bioluminescence emissions from space is scheduled for the seven-day new moon period around September 28, 1981, using the Dynamics Explorer spacecraft DE-1. A visible wavelength imaging photometer carrying a wide-band ( $\Delta\lambda = 44 \text{ nm}$ ) interference filter at 482 nm with a photometric sensitivity per image pixel of  $5.8 \times 10^{-7} \text{ W/m}^2/\text{count}$  will be used. No results are reported in this abstract.

188. Geiger, Mark L. (1982). A Prototype Bioluminescence Photometer. Naval Oceanographic Office, Stennis Space Center, Mississippi, Technical Report TR-280.

This document describes the Naval Oceanographic Office's Bioluminescence Photometer System, a vertically lowered device that records flashes of light produced when small bioluminescent marine organisms are pumped into a turbulent flow regime chamber where they are viewed by a photomultiplier tube. The history and performance of this device are documented in this report. The combined results of experience at sea and engineering performance evaluations suggest the following. (1) The present instrument is a useful tool for mapping dinoflagellate bioluminescence capabilities within the upper ocean. (2) A recent modification (based on a 12-conductor set of winch slip rings) allowed continuous profiles of dinoflagellate light production

to be recorded without significant decreases in sensitivity or signal degradation by noise. (3) The present instrument is not useful for underway work or for measuring light produced by organisms of approximately 400 $\mu$  in length and larger (thus excluding the larger copepods and practically all euphausiids, fishes, squids, etc.). (4) Several improvements can be made on the present device by experimenting with underway systems and with chamber sizes, shapes and flow regimes; by altering rates of pumping; and by deviating from the present chart record counting of flashes to an automated data retrieval system. The system would be based not on individual organism performance but on the maximally stimulated bioluminescent light produced within a unit volume of seawater. (5) Extrapolation beyond the improvements suggested implies that different kinds of measurement systems will eventually be required to study the large-animal luminescence that is now subject to instrument avoidance problems. Although they are subject to animal avoidance problems, pumping photometers are, nevertheless, likely to play important roles in future schemes for measuring bioluminescence at sea. This is true because pumping photometers do yield information on dinoflagellate luminescence, and is more important than it would be if only the global ubiquitousness of dinoflagellates were considered. Specifically, dinoflagellate luminescence is an indirect index of a region's potential for large-animal luminescence through the dinoflagellates' link with regional fertility and through the dinoflagellates' ability to trigger secondary luminescence in larger organisms.

189. Gitel'zon, I. I. (1982). Bioluminescence as General Oceanic Phenomenon and the Possibilities of Its Usage for the Analysis of the Marine Ecosystem. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Akad. Nauk USSR, Krasnoyarsk, pp. 31-59.

Generalized conclusions regarding oceanic bioluminescence are presented. Bathypotometers (of different types for specific purposes) are the principal instruments for measurement. Bioluminescence is universal in the oceans and at all depths at night, but is almost entirely absent from the euphotic zone during the day. It is highly patchy, on a scale of hundreds of meters to tens of kilometers horizontally, and highly stratified vertically, correlating roughly with biomass and productivity. It occurs

characteristically in the form of flashes, with spontaneous emission representing less than 1% of the output, and exhibits a circadian rhythm. It does not occur at salinities less than 10-12‰, but will occur at all customary ocean temperatures. Dinoflagellates and crustacea are the major producers, with saprophytic bacteria contributing about 10% in the open ocean and 60% in coral atoll lagoons.

190. Gitel'zon, I. I. (1984). Symbiotic and Pathogenic Luminous Bacteria. In *Luminescent Bacteria* (English translation of *Sveryashchiyesya Bakterii*, Ye. N. Kondrat'yeva, ed., Izdatel'stvo "Nauka," Moscow), pp. 31-69. JPRS-UBB- 85-018-L, 31 October 1985.

A short account of the discovery of symbiosis between luminous bacteria and higher organisms is given. Various fish light organs are described in detail, along with light regulation mechanisms and the role of light emission in fish behavior and ecology. The symbiosis of luminous bacteria with cephalopods and tunicates is briefly discussed. A description of infections by pathogenic luminous bacteria is used as the basis for a discussion of possible natural bioengineering solutions to the problem of maintaining the symbiotic luminous bacterial cultures in photophores.

191. Gitel'zon, I. I. and V. S. Filimonov (1980). Bioluminescence of a Coral Reef. *Biol. Morya* 6(5):45-51 (Russian) :277-282 (English).

Instrumental recording and visual observations of bioluminescence of a coral reef are carried out. Polychaetes and sponges outnumber other organisms in bioluminescence. Spontaneous bioluminescence of the coral reef is comparatively weak but regular. Mechanical stimulation elicits a response in the form of an intensive light flash.

192. Gitel'zon, I. I. and V. S. Filimonov (1980). Bioluminescence of a Coral Reef. *Trudy Inst. Okeanol. Akad. Nauk SSSR* 90:58-62 (Russian).

A specially designed bathypotometer is used to measure the bioluminescence of benthic organisms in situ. These measurements are combined with laboratory measurements of the emission parameters of selected organisms. It is concluded that an estimate of the distribution of luminous benthic organisms can be obtained solely from flash signal data, but that the present instrumentation is insufficient for that purpose.

193. Gitel'zon, I. I. and V. S. Filimonov (1980). The Use of Bioluminescence Probing for Determination of the Biological Structure of the Water Column. *Trudy Inst. Okeanol. Akad. Nauk. SSSR* 90:244-251 (Russian).

Problems concerning structural variations in the vertical distribution of the bioluminescence field are discussed. During the 18th cruise of the R/V *Dmitry Mendeleev* the vertical distribution of the bioluminescence field is used to characterize the biological stability of the entire community along the 140°E meridian between the equator and 10°N latitude. Data obtained on this cruise are compared with data obtained on the 38th cruise of the R/V *Vityas*. The transitions between the day and night distributions at dawn and dusk require about 2 hours each so that the period during which the bioluminescence probe technique can be used is limited. Studies near islands confirm that bioluminescence probing may be used to find small scale inhomogeneities in plankton quantity and distribution.

194. Gitel'zon, I. I., V. S. Filimonov and V. M. Musonov (1981). Bioluminescence in Surface Water of Central Arctic in Spring. *Dokl. Akad. Nauk USSR* 256:(3)723-726.

Bioluminescence is measured through a hole cut in Arctic ice using a shielded bathyphotometer. Measurements are made at the beginning of solar summer with the sun beneath the horizon in overcast, twilight conditions. Luminescence is observed from 10 to 66 m deep, with an intensity of about  $8 \times 10^7$  quanta/sec. Thin layers of activity occur.

195. Gooch, Van D. (1985). Effects of Light and Temperature Steps on Circadian Rhythms of *Neurospora* and *Gonyaulax*. In *Temporal Order*, L. Rensing and N. I. Jaeger, eds., New York: Springer-Verlag, pp. 232-237.

Spontaneous glow peaks for *Gonyaulax* phase to the last light onset when the last dark period exceeds six hours. When the last dark period is in the 0-12 hour range, large phase advances can be achieved.

196. Gooch, Van D. and William Vidaver (1981). Kinetic Analysis of the Influence of Hydrostatic

Pressure on Bioluminescence of *Gonyaulax polyedra*. *Photochem. Photobiol.* 31:397-402.

Hydrostatic pressure was used as a probe to examine control mechanisms of bioluminescence in *Gonyaulax polyedra*. The initial effect of a pressure increase step is both to increase the intensity of the continuous light emission (glow) of the entire cell population and to increase the frequency of discrete flashes arising from single cells. Following the pressure application, however, the glow does not merely attain a new level but rather goes through various transient changes, whereby the kinetics of these changes are faster with a given higher pressure. A qualitative fit to several aspects of the pressure induced glow kinetics was generated by a simple reaction rate theory model. The effect of pressure upon the circadian rhythm control of bioluminescence was also investigated with the result being that no significant influence was observed under the experimental conditions.

197. Gordienko, A. P., M. N. Lebedeva and Yu. N. Tokarev (1980). Bacterioplankton Number in Bioluminescence Extrema in Some Seas of the Mediterranean Sea Basin. *Ekol. Morya* (Kiev) 80:15-21 (Russian).

Data on the total bacteria number at the depths of bioluminescent field extrema are obtained for the euphotic zone of the Black, Aegean, Ionian and Tyrrhenian Seas. A correlation is established between the qualitative development of the bacterial life and bioluminescence intensity indices ( $r = 0.74$  when  $p = 95\%$ ).

198. Gordon, A. S. and John C. Makemson (1985). Total Energy Flux from Luminous Bacteria. *Abstr., Ann. Meet. Am. Soc. Microbiol.* 85:219.

**ABSTRACT.** A total energy budget for cultures of *Vibrio harveyi* growing in minimal medium is determined. Bioluminescence accounts for only 0.007% of the heat released. In complex medium, bioluminescence is only 0.01 to 0.03% of the total heat released.

199. Goto, Toshio (1980). Bioluminescence of Marine Organisms. In *Marine Natural Products, Chemical and Biological Perspectives*, Vol. 3, Paul J. Scheuer, ed., New York: Academic Press, pp. 179-222.

The bioluminescence of marine organisms is comprehensively but concisely reviewed. Chemical and physiological mechanisms of light production and control are emphasized and organisms are classified according to whether they exhibit a luciferin-luciferase reaction or a photoprotein reaction, or utilize symbiotic luminous bacteria.

200. Goto, Toshio (1982). Mechanism of Bioluminescence in Biology. In *Fuoto Baiorogiji: Koseiri Gensho no Shoki Katei*, M. Yoshida, ed., Kodansha Saientifiku, Tokyo, pp. 61-76 (Japanese).

The chemical mechanism of the bioluminescence reactions in fireflies and *Cypridina* is described and shown. A model for the electronic pathway is presented. The kinetics and energetics of key reaction stages are tabulated.

201. Greenberg, E. P., J. Woodland Hastings and Shimon Ulitzur (1979). Induction of Luciferase Synthesis in *Beneckea harveyi* by Other Marine Bacteria. *Arch. Microbiol.* 120:87-91.

It has been previously demonstrated that luciferase synthesis in the luminous marine bacteria, *Beneckea harveyi* and *Photobacterium fischeri* is induced only when sufficient concentrations of metabolic products (autoinducers) of these bacteria accumulate in growth media. Thus, when cells are cultured in a liquid medium, there is a lag in luciferase synthesis. A quantitative bioassay for *B. harveyi* autoinducer was developed, and it was shown that many marine bacteria produce a substance that mimics its action, but in different amounts (20% to 130% of the activity produced by *B. harveyi*), depending on the species and strain. This is referred to as alloinduction. None of the bacteria tested produced detectable quantities of inducer for *P. fischeri* luciferase synthesis. These findings may have significance with respect to the ecology of *B. harveyi* and *P. fischeri*.

202. Greenblatt, P. R., D. F. Feng, Alberto Zirino and Jon R. Losee (1982). Observations of Bioluminescence in the Euphotic Zone of the California Current. *EOS* 63(45):944-945.

**ABSTRACT.** During July, 1982, bioluminescence in the California Current showed a depth maximum at the surface at night and between 30-40 m during the day. Nighttime bioluminescence intensity was up to 40 times daytime intensity. The vertical

distribution was not associated with thermal structure, but broadened during a period of high wind. Day-night spectral differences suggest different populations of causative organisms.

203. Greenblatt, P. R., D. F. Feng, Alberto Zirino and Jon R. Losee (1984). Observations of Planktonic Bioluminescence in the Euphotic Zone of the California Current. *Mar. Biol.* 84:75-82.

The distributions of bioluminescence, temperature, salinity, oxygen, pH and chlorophyll *a* were measured at 10-m intervals, to a depth of 100 m at a station (33°46'N;119°36'W) in the California Current from 17 to 20 July 1982. The distribution of bioluminescence showed a marked day-night change, which was consistent over the sampling period. The nighttime maximum was at the surface and the daytime maximum was between 30 and 40 m. The shapes of the day and night distributions were independent of the absolute intensity of bioluminescence and were also insensitive to advection, as inferred from changing temperature-salinity relationships. The nighttime depth distribution broadened during a period of high wind. Day to night differences in the color spectrum at the depth of maximum bioluminescence suggest that the luminescent organisms differed from day to night.

204. Griswold, Carolyn, Jon R. Losee and David Lapota (1983). Correlation of Zooplankton Community Structure and Measured Bioluminescence Throughout the Water Column Using a Manned Submersible. *EOS* 64(52):1102.

**ABSTRACT.** Nineteen dives ranging in depth from 200 to 600 m, were made using the Johnson/Sea Link in the Gulf of Maine. Bioluminescence and various physical and chemical oceanic parameters were measured and organisms were collected and identified. Results indicated that the pumped bathyphotometer system sampled only small organisms such as copepods and dinoflagellates but not larger, more active or fragile zooplankters such as euphausiids and gelatinous organisms. This result suggests that water column bioluminescence is underestimated when standard measuring techniques are employed.

205. Grober, Matthew S. (1985). Luminescence in *Ophiopsila riiseri*: A Test of Possible Functions. *Abstr., Western Soc. Naturalists 66th Ann. Meet.* 66:37.

**ABSTRACT.** Bioluminescence in the brittlestar *Ophiopsila riisei* acts as an effective anti-predatory agent and thus maximizes *Ophiopsila* feeding efficiency and decreases mortality or damage due to predators. Secondary effects on the community structure and behavior of coexisting species probably also occur.

206. Grober, Matthew S. (1987). Luminescence in *Renilla köllikeri* (Cnidaria:Pennatulacea) Inhibits Decorating Behavior and Predation in Juvenile *Loxorhynchus grandis* (Crustacea:Brachyura). *Abstr., Western Soc. Naturalists 69th Ann. Meet.* 69:20.

**ABSTRACT.** The bright luminous flashes produced by *Renilla* upon mechanical stimulation deter predation and reduce decorating behavior by *Loxorhynchus grandis*, a crustacean that commonly preys upon sea pansies, and may deter other nocturnal predators as well.

207. Grober, Matthew S. (1987). Ophiuroid Luminescence: A Keystone Phenomenon in Nocturnal Reef Communities. *Amer. Zool.* 27(4):102A.

**ABSTRACT.** Actively foraging predators increased avoidance and decreased predatory behavior in response to contact-initiated flashes from *Ophiopsila riisei*. Small scavengers and cleaner shrimp showed no behavioral changes. These differences suggest that luminescent ophiuroids differentially affect the distribution of predatory and prey organisms.

208. Grober, Matthew S., Charles P. Galt and Paul F. Sykes (1981). Morphological Correlates of Bioluminescence in Appendicularians (Urochordata, Larvacea). *Abstr., Western Soc. Naturalists 62nd Ann. Meet.* 62:21.

**ABSTRACT.** Houses of six species of larvaceans (two, *Oikopleura rufescens* and *Stegosoma magnum*, here reported for the first time) luminesce upon mechanical stimulation from fluorescent granules in the house rudiment near the oral glands. *Megalocercus huxleyi* lacks such granules and oral glands and does not luminescence. It is predicted that only larvacean species possessing oral glands and rudiment granules will emit light.

209. Grogan, Dennis W. (1984). Interaction of Respiration and Luminescence in a Common Marine Bacterium. *Arch. Microbiol.* 137:159-162.

Investigators have proposed for some time that bacterial luciferase forms a shunt around the pathway of respiratory electron transport. Certain physiologic evidence for coupling between luminescence and respiration has supported such a view. In this study, *Vibrio harveyi* cells were monitored for luminescent responses to artificial manipulation of respiratory electron flow. The effects of cyanide under aerobic and anaerobic conditions confirmed that luminescence and respiration compete for oxygen. The effects of an uncoupler of oxidative phosphorylation indicated that luminescence and respiration compete for a common reductant. Treatment with uncoupler also induced aldehyde deficiency in vivo.

210. Gurevich, V. B., A. V. Svetlakov, L. Yu. Popova and A. N. Shenderov (1986). Glutamate Synthesis Control in *Vibrio harveyi*. *Microbiology (USSR)* 55(1):77-79 (Russian) :66-68 (English).

Glutamate plays an important role in the osmoregulation of the luminescent bacterium *Vibrio harveyi*. Its synthesis was shown to be catalyzed by NADH-dependent glutamate dehydrogenase (GDH) and glutamate synthase. The activity of GDH decreased on addition of arginine or proline into the medium and was highly dependent on the sodium chloride content. One of the physiological functions of GDH is believed to be the provision of adaptive glutamate synthesis in response to medium salinity increase. An inverse relation between the level of bioluminescence and GDH activity was observed. This may be explained by competition between the luminescence system and GDH for NADH.

211. Haas, Elisha and J. Woodland Hastings (1982). Bacterial Bioluminescence from Single Cells Exhibits No Oscillation. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyorsk: Akad. Nauk USSR, pp. 337-348.

Although an oscillation with a frequency of 8 cycles/s has been reported from small colonies of luminous bacteria, no such oscillation is observed from single cells. Instead, the light appears entirely continuous.

212. Hada, H. S., J. Stemmler, M. L. Grossbard, P. A. West, Catherine J. Potrikus, J. Woodland Hastings and Rita R. Colwell (1985). Characterization of Non-O1 Serovar *Vibrio cholerae* (*Vibrio albensis*). *System. Appl. Microbiol.* 6:203-209.

Eight luminescent strains of *Vibrio*, isolated from diverse geographic locations, were classified as serovar non-01 *Vibrio cholerae* by morphological, physiological and numerical taxonomy analysis. All isolates possessed overall DNA base composition of 47-48 mol percent guanine plus cytosine. Based on DNA-DNA hybridization, luminescent strains, as a group, exhibited  $\geq 70\%$  base sequence complementarity with serovar 01 *V. cholerae* and  $< 40\%$  with other *Vibrio* spp. examined. Results of the hybridization studies confirm that *Vibrio albensis* is synonymous with *V. cholerae* and distinct from other luminescent vibrios. In addition, the luminescence system in *V. cholerae* was investigated as a characteristic of *V. cholerae*, to provide new information for the description of the species. In most cases, autoinducer from *V. harveyi* strain 392S3 induced synthesis of the luminescent system in strains of *V. cholerae* and vice versa. Unlike the case of *V. harveyi* 392S3, in *V. cholerae* strain P287 the synthesis of the luminescent system is impaired at low oxygen and, also in contrast to *V. harveyi* strain 392S3, dark mutants (K variants) of the three *V. cholerae* examined occur at extremely low frequency.

213. Häder, Donat-Peter and Manfred Tevini (1987). Bioluminescence and Chemiluminescence. In *General Photobiology*, New York: Pergamon Press: pp. 90-97.

A suggestion of the wide variety of light-producing organisms is given. The light-producing biochemical reactions in bacteria, fireflies and coelenterates are presented in broad detail and the structures of luciferins from coelenterates, *Cypridina* and fireflies are shown.

214. Halberg, F., J. Woodland Hastings, G. Cornelissen and Hellmuth Broda (1985). *Gonyaulax polyedra* "Talks" Both "Circadian" and "Circaseptan." *Chronobiologia* 12:185.

**ABSTRACT.** In addition to circadian (about 24-hour) rhythms of bioluminescence, *Gonyaulax polyedra* exhibits circaseptan (about 7-day) rhythms. Mixed cultures of populations originally on different phases show merging of bioluminescence glow peaks for both rhythms. This finding suggests cellular communications on both the circadian and circaseptan levels.

215. Hamman, John P., William H. Biggley and Howard H. Seliger (1981). Action Spectrum for the

Photoinhibition of Bioluminescence in the Marine Dinoflagellate *Dissodinium lunula*. *Photochem. Photobiol.* 33:741-747.

The fractional photoinhibition of the mechanically stimutable bioluminescence in the vacuolar dinoflagellate *Dissodinium lunula* is proportional to the logarithm of the exposure. The action spectrum for this photoinhibition has been determined by measuring threshold exposures in absolute units of photons  $\text{cm}^{-2}$ . The threshold exposure at the wavelength of maximum sensitivity, 450 nm, was  $2 \times 10^{12}$  photons  $\text{cm}^{-2}$ . The action spectrum is consistent with absorption by a blue light receptor pigment shielded by a nonphotoactive pigment which absorbs in the region of the bioluminescence emission spectrum. It is suggested that there may be some selective advantage for this absorbing pigment in the vacuolar dinoflagellates in order to prevent the organisms from being photoinhibited by their own bioluminescence.

216. Hamman, John P., William H. Biggley and Howard H. Seliger (1981). Photoinhibition of Stimulable Bioluminescence in Marine Dinoflagellates. *Photochem. Photobiol.* 33:909-914.

Different genera of bioluminescent photosynthetic dinoflagellates exhibit different mechanisms for the inhibition of stimutable bioluminescence during the daylight. These are (1) reduction in bioluminescence capacity, (2) increased refractoriness to mechanical stimulation, and (3) inhibition of transmission of signals from mechanical receptor sites to bioluminescence emission sites. The increase in stimutable bioluminescence that in nature mirrors the decrease in sunlight intensity prior to sunset is dependent upon the logarithm of the ambient irradiation intensity. Photoinhibition of bioluminescence in all species examined except *Gonyaulax polyedra* is the result of absorption of light in the blue region of the spectrum.

217. Hamman, John P. and Howard H. Seliger (1979). Dinoflagellate Bioluminescence: Luciferase Turnover in the Absence of a Luciferin Binding Protein. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 65.

**ABSTRACT.** No luciferin binding protein is found in four species of dinoflagellates belonging to the genus *Pyrocystis*. From these species a soluble luciferase-luciferin complex can be isolated, which emits a rapid flash upon a pH jump, followed by

further light emission for several seconds. With excess luciferin, total light emission is independent of luciferase concentration. These observations suggest flash control by the turnover rate of luciferase and the availability of free luciferin.

218. Hamman, John P. and Howard H. Seliger (1982). The Chemical Mimicking of the Mechanical Stimulation, Photoinhibition, and Recovery from Photoinhibition of Bioluminescence in the Marine Dinoflagellate, *Gonyaulax polyedra*. *J. Cell. Physiol.* 111 (3):315-319.

Mechanically stimuable bioluminescence and photoinhibition of sensitivity to mechanical stimulation in the marine dinoflagellate *Gonyaulax polyedra* can be mimicked by a number of cations, proportional to the logarithm of their external concentrations. The data are consistent with mechanical stimulability as a membrane depolarization resulting in an increase in  $H^+$  ions at bioluminescence sites and with photoinhibition as a hyperpolarization of the cell membrane.

219. Hampton, I., J. J. Agenbag and David L. Cram (1979). Feasibility of Assessing the Size of the South West African Pilchard Stock by Combined Aerial and Acoustic Measurements. *Fish. Bull. S. Afr.* 11:10-22.

A method is being developed for determining the stock size of the South West African pilchard from nighttime aerial measurements of shoal area combined with synchronous acoustic determinations of fish density within the shoals. An analysis of the possible errors in an aerial and an acoustic survey, conducted independently, suggests that by combining the two methods it should be possible to estimate the relative stock size with a precision of at least 50% with 95% confidence. It is estimated that the random errors and biases would contribute up to 20% and 30%, respectively, to the total error. Meaningful assessments of absolute abundance would probably be precluded by large uncertainties in any value assumed for the mean acoustic target strength of the fish.

220. Haneda, Yata (1980). Luminescent Fish with Open-type Glands Containing Luminous Bacteria or Luminous Substances of Ingested Crustaceans. *Sci. Rep't Yokosuka City Mus.* 27:5-12.

Fish luminescent systems may be classified into four types: (1) well-developed photophores and intracellular bioluminescence; (2) extracellular luminescence by means of a luminous secretion; (3) a

luminous organ open to the outside containing symbiotic luminous bacteria; and (4) a luminous organ open to the outside containing ingested luminous material from crustaceans. Fish of the third type are widely distributed taxonomically and environmentally. Bacteria have been cultured from all except members of the family Anomalopidae and *Leiognathus elongatus*. Infection is believed to occur in the early larval stages from free-living bacteria in seawater, but this mode has been demonstrated experimentally only for *Siphamia versicolor*. The fourth type of luminescence system is found only in fish of the families Pempheridae and Apogonidae (except *Siphamia*). The light organs either are comprised of part of the digestive tract or are connected to it by ducts. Luciferin and luciferase extracted from these organs cross-react with those of ostracod crustaceans of the genus *Cypridina* to produce light and the luciferins of both the fish and crustaceans appear chemically identical or closely related. A taxonomic classification of luminous fishes is included.

221. Haneda, Yata (1982). Evolved Luminous Species from Non-luminous Species Belonging to the Family Apogonidae. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 60-68.

Fishes of the family Apogonidae all contain luminous organs open to the outside environment. In the genus *Siphamia* this organ contains symbiotic luminous bacteria; in all other genera the light organ contains ingested luminous substances from crustaceans. On a morphological basis these luminous systems may be divided into four types: (1) *Siphamia* type (2) *Apogon ellioti* type, which consists of one luminous organ connected to the second loop of the intestine and two luminous organs connected to the rectum by ducts; (3) *Archamia lineolata* type, in which the second loop of the intestine and the pyloric caeca comprise the luminous organ; and (4) *Rhabdamia cypselura* type, in which the luminous organ is formed from the distal ends of the first pair of pyloric caeca connected to a pair of transparent lens-like organs located in the ventral-lateral wall of the body cavity and through which light is transmitted to the outside. These fish may have evolved into luminous species through evolutionary pressures from luminous bacteria or crustaceans in their diet.

222. Haneda, Yata (1986). On a New Type of Luminous Fishes and Squids Ingested Luminescence. In *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes*, Teruya Uyeno, Ryoichi Arai, Toru Taniuchi and Keiichi Matsuura, eds., Tokyo: The Ichthyological Society of Japan, pp. 838-839.

Luminescent systems in fish and squids may be classified into three types: (1) well-developed, self-luminous organs; (2) luminous organs containing symbiotic luminous bacteria; and (3) luminous organs containing ingested luminous substances from crustaceans. Members of the second category include fish of the families Acropomidae, Anomalopidae, Argentinidae, Leiognathidae, Macrouridae, Monocentridae, Moridae, and Trachichthyidae and the genus *Siphamia* of the family Apogonidae, and mysid squids. Members of the third category include fish of the families Apogonidae (except *Siphamia*), Batrachoididae (genus *Porichthys*) and Pempheridae, and the squids *Eucleoteuthis luminosa* and *Sepiolina nipponensis*.

223. Hardeland, Rüdiger (1980). Effects of Catecholamines on Bioluminescence in *Gonyaulax polyedra* (Dinoflagellata). *Comp. Biochem. Physiol.* 66C:53-58.

In the dinoflagellate *Gonyaulax polyedra*, epinephrine stimulated the bioluminescence up to 470-fold. This action was time- and dose-dependent and relatively specific, since other catecholamines (natural or synthetic) turned out to be much less effective. Propranolol evoked a short initial stimulation followed by normal and finally subnormal intensities of bioluminescence. The effect of epinephrine was not inhibited by phentolamine, but was totally blocked by propranolol. Although this might suggest at the first view that epinephrine would act through a sort of  $\beta$ -adrenergic mechanism, similarities in the effects of propranolol with those of quinidine favour another interpretation, namely that propranolol acts by changes of membrane fluidity. Both propranolol and quinidine completely suppressed the circadian increase in bioluminescence.

224. Hardeland, Rüdiger (1982). Circadian Rhythms of Bioluminescence in Two Species of *Pyrocystis* (Dinophyta). Measurements in Cell Populations and in Single Cells. *J. Interdiscipl. Cycle Res.* 13(1):49-54.

Endogenous circadian rhythms of spontaneous bioluminescence are demonstrated in two recently collected dinoflagellate strains, *Pyrocystis elegans* strain ME 8 and *Pyrocystis* cf. *acuta* strain ME 9. The rhythms free-run in DD for several periods, but are readily damped out in LL. The emitted light intensity allows measurements in single cells by means of a scintillation spectrometer. With regard to the periodicity of spontaneous bioluminescence, the two species differ from other cultured strains of *Pyrocystis* species such as *P. lunula* and *P. fusiformis*, which only show rhythms of induced bioluminescence.

225. Hardeland, Rüdiger, Ivonne Balzer, Norbert Stahr and Gerhard Holzapfel (1980). Phase Shifting of the Circadian Clock in *Gonyaulax polyedra* by Puromycin and Quinidine. *Eur. J. Cell. Biol.* 22(1):496.

**ABSTRACT.** Continuous exposure of *Gonyaulax polyedra* to low concentrations of the protein synthesis inhibitor puromycin delayed and to high concentrations abolished, the free-running circadian rhythm of bioluminescence. Pulses either delayed the rhythm or were ineffective, depending on the circadian time of administration. Quinidine advanced the rhythm in constant exposure and advanced or delayed it slightly in the pulses. These findings suggest that protein synthesis and membrane manipulation affect the fundamental oscillator.

226. Hardeland, Rüdiger and Pernille Nord (1984). Visualization of Free-Running Circadian Rhythms in the Dinoflagellate *Pyrocystis noctiluca*. *Mar. Behav. Physiol.* 11:199-207.

In *Pyrocystis noctiluca* circadian rhythms can be observed at cellular level directly in the light microscope. A rhythm of chloroplast expansion and contraction was visualized by autofluorescence of chlorophyll; a concomitant rhythm in the intracellular distribution of bioluminescent microsources was seen upon stimulation of cells by acid. Measurements of bioluminescence by means of a scintillation counter revealed the absence of a rhythm in spontaneous bioluminescence; however, the existence of a rhythmicity in stimulated bioluminescence was demonstrated by treating cells with acid.

227. Hart, Russell C., John C. Matthews, Kazuo Hori and Milton J. Cormier (1979). *Renilla reniformis*

**Bioluminescence: Luciferase-Catalyzed Production of Nonradiating Excited States from Luciferin Analogues and Elucidation of the Excited State Species Involved in Energy Transfer to *Renilla* Green Fluorescent Protein.** *Biochemistry* 18:2204-2210.

A number of coelenterate-type luciferin analogues with structural changes in the p-hydroxyphenyl and p-hydroxybenzyl substituents have been synthesized. During chemiluminescence, each of the analogues produces a blue emission arising from the singlet excited state of the corresponding oxyluciferin monoanion. During bioluminescence two emissions are observed with coelenterate-type luciferin and some of its analogues. One of these arises from the amide monoanion ( $\lambda_{\text{max}}=480$  nm) and the other arises from the neutral species of oxyluciferin ( $\lambda_{\text{max}}=395$  nm). Certain analogues produce both emissions, while others produce only the near-ultraviolet emission. Structural changes in the p-hydroxyphenyl substituent result in complete or nearly complete elimination of emission from the monoanion, resulting in over a 100-fold reduction in bioluminescence quantum yield. Structural changes in the p-hydroxybenzyl substituent do not have a significant effect on the emission spectrum but decrease the luciferase turnover number approximately 25-fold. The large decrease in the bioluminescence quantum yield observed with some of the analogues can be overcome by addition of green fluorescent protein (GFP). GFP forms a rapid equilibrium complex with luciferase and is known to function in this system as an efficient energy-transfer acceptor. Spectral analyses have shown that radiationless energy transfer occurs from the singlet excited state of the oxyluciferin monoanion and not from the neutral excited species. The energy-transfer data suggest that the luciferase-bound monoanion singlet excited state can be quenched by solvent and/or protein functional groups. Energy transfer to GFP can apparently favorably compete with this quenching process. Lifetime measurements have shown that the rate of energy transfer must be at least  $3 \times 10^8 \text{ sec}^{-1}$ .

228. Hashimoto, K., M. Aoki and Haruo Watanabe (1985). Bioluminescence in the Ascidian, *Clavelina miniata*. II. Classification and Ultrastructure of the Test Cells. *Zool. Sci. (Tokyo)* 2(6):929.

**ABSTRACT.** Test cells in the tunic of *Clavelina miniata* may be classified into three groups based on cytoplasmic inclusions. Only Type II cells

emit light. This type comprises 80% of the test cells and is characterized by green granules and large vacuoles containing fibrous materials. 65% of Type II test cells occur near the cuticle. Symbiotic luminous bacteria appear to be absent.

229. Hastings, J. Woodland (1978). Bacterial and Dinoflagellate Luminescence Systems. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 129-170.

This article thoroughly reviews the biochemistry of luciferin, luciferases and the bacterial luminescence system as a whole. It compares characteristics of native luciferase and luciferases from several mutant strains and describes photoexcitation of luciferase. A reaction pathway is proposed and an emitting species of molecule is postulated. Energy requirements are established. Autoinduction and emission control through arginine stimulation, catabolite repression and oxygen regulation are described. Possible ecological functions are discussed. The two luminescence systems in dinoflagellates, the soluble and particulate systems, are discussed and a model of flashing is proposed.

230. Hastings, J. Woodland (1979). Biological Diversity and Chemical Mechanisms in Bioluminescence. In *Proc., Int. Symp. on Analytical Applications of Bioluminescence and Chemiluminescence*, E. Schram and P. Stanley, eds., Westlake Village (California): State Printing and Publishing, Inc., pp. 1-31.

A short table of luminous organisms is given and the habitats and appearance of luminescence in most of the major biological groups are discussed qualitatively. The biological functions of bioluminescence (attracting prey, defending against predators and communication) are exemplified with respect to selected organisms. Physiological control mechanisms are described, with emphasis on autoinduction in bacteria. Emission spectra for a number of organisms are depicted and compared along with the kinetics of the dinoflagellate flash. The biochemical reaction mechanisms for several groups of organisms are described briefly and that of bacteria is discussed in detail.

231. Hastings, J. Woodland (1982). Current Perspectives in Bioluminescence: Chemical Mechanisms and Biological Functions. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and

J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 16-30.

Two generalized chemical mechanisms for bioluminescence are discussed. The possibility of cross phylogenetic gene transfer as an explanation for similar luciferins in taxonomically distant species is raised. Possible biological functions for bioluminescence are generalized into three categories: communication (including mating); offense (predation); and defense (avoiding predation).

232. Hastings, J. Woodland (1983). Biological Diversity, Chemical Mechanisms and the Evolutionary Origins of Bioluminescent Systems. *J. Mol. Evol.* 19:309-321 (abstract published in *Abstr., 15th Pacific Science Cong.* 1:96-97).

A diversity of organisms are endowed with the ability to emit light and to display and control it in a variety of ways. Most of the luciferins (substrates) of the various phylogenetically distant systems fall into unrelated chemical classes and, based on still limited data, the luciferases (enzymes) and reaction mechanisms are distinctly different. Based on its diversity and phylogenetic distribution, it is estimated that bioluminescence may have arisen independently as many as 30 times in the course of evolution. However, there are several examples of cross-phyletic similarities among the substrates; some of these may be accounted for nutritionally, but in other cases they may have evolved independently.

233. Hastings, J. Woodland (1983). Chemistry and Control of Luminescence in Marine Organisms. *Bull. Mar. Sci.* 33(4):818-828.

Bioluminescence occurs in very many different marine organisms. The reaction is an enzyme (luciferase) mediated chemiluminescence in which a substrate is oxidized by molecular oxygen; energy thereby available is conserved in the form of a molecule in an electronically excited (singlet) state which subsequently emits light. The luciferins and luciferases utilized in different organisms may be very different, but all known luciferases may be classed as oxygenases, involving peroxides (in some cases ring peroxides) as intermediates; in some cases electron transfer has been postulated in the terminal steps leading to excitation. The cellular control of bioluminescent reactions involves special mechanisms such as the sequestration of substrate by a binding

protein or the accumulation of a reaction intermediate and a triggering step, as for example by  $H^+$  or  $Ca^{++}$ .

234. Hastings, J. Woodland (1985). Biochemistry and Subcellular Localization of Luminescence in Marine Dinoflagellates. *Photochem. Photobiol.* 41(S):16S.

**ABSTRACT.** After mechanical or electrical stimulation, luminous marine dinoflagellates emit light flashes of about  $10^{10}$  photons lasting about 100 ms from autofluorescent subcellular organelles. These organelles appear to correspond to the luminous particulate fraction in cell extracts called scintillons. Scintillons exhibit the same biochemical components as luminescence in the soluble fraction, i.e., luciferase, luciferin, and a luciferin-binding protein. Scintillons are identified with the autofluorescent organelles through the fluorescent characteristics of luciferin and direct observation using image-intensified video microscopy. Ultrastructural studies have been performed using immunogold labeling. The possibility of two different classes of light-emitting organelles is raised.

235. Hastings, J. Woodland (1986). Distributions, Activities and Functions of Marine Luminescent Bacteria. *Fourth Int. Symp. Microbiol. Ecology.*

**ABSTRACT.** Theories on the function of bioluminescence in luminous bacteria are presented. The biochemical role of luciferase in the bacterial energy system is explained. Cloning and gene mapping are suggested as a means of determining molecular aspects of the control of luminescence.

236. Hastings, J. Woodland (1986). Bioluminescence in Bacteria and Dinoflagellates. In *Light Emission by Plants and Bacteria*, Govindjee, Jan Ames and David Charles Fork, eds., New York: Academic Press, pp. 363-398.

Light emission in living organisms may be due either to prior absorption of light (photoluminescence) or to an exergonic chemical reaction (chemi- or bioluminescence). In photosynthesis the chemical species formed in the primary step following light absorption are similar to those postulated to be the penultimate states in many chemiluminescent and bioluminescent reactions. Mechanistically, bioluminescence may be viewed as the reverse of photosynthesis. Bioluminescence occurs in organisms of many different phyla, including the bacteria and dinoflagellates described here. Most of the enzymes

and substrates (luciferases and luciferins) are unrelated, indicative of evolutionarily different origins. In the bacteria light emission is continuous and occurs as the result of a reaction which shunts the respiratory pathway: a mixed-function oxidation of reduced flavin and long-chain aliphatic aldehyde by molecular oxygen. In dinoflagellates light emission is distinctly different. The substrate (luciferin) is an open-chain tetrapyrrole which bears a similarity to chlorophyll and its oxidation results in luminescence. This occurs primarily in the form of flashes emitted from subcellular organelles. In the living cell control of the reaction and of the light flash is postulated to involve pH changes.

237. Hastings, J. Woodland (1986). Bioluminescence. In *Encyclopedia of Science and Technology* (6th ed.) 2:545-550 (also in 1986 *Yearbook*, pp. 123-125), New York: McGraw-Hill.

Bioluminescence is defined and briefly described. The physics and chemistry of the light-producing reaction are outlined, especially for fireflies, *Cypridina* and bacteria and chemical structures are depicted for those three organisms. The diversity of luminous organisms is briefly explored and some biological functions are given. Theories on the origin and evolution of bioluminescence are mentioned.

238. Hastings, J. Woodland (1987). Dinoflagellate Bioluminescence: Biochemistry, Cell Biology and Circadian Control. In *Bioluminescence and Chemiluminescence: New Perspectives*, J. Schölerich, R. Andreeson, A. Kapp, M. Ernst and W. G. Woods, eds., New York: John Wiley and Sons, pp. 343-350.

This paper summarizes recent progress on the bioluminescent system in marine dinoflagellates, especially *Gonyaulax polyedra*. Light emission involves oxidation of the luciferin, an unique open chain tetrapyrrole molecule, catalyzed by the luciferase, but the site of oxygen addition and the identity of the light emitting moiety are not known. Luciferin fluorescence has been used to identify and locate emitting granular microsources, called scintillons, within the cytoplasmic compartment of the cell. Circadian rhythms of luciferin, luciferase and luciferin-binding protein are identified.

239. Hastings, J. Woodland, Jean-Marie Bassot and Marie-Thérèse Nicolas (1987). Intracellular Localization Control of Luminescent Emissions. *Ann. New York Acad. Sci.* 503 (Endocytobiology III):180-186.

Although sophisticated light organs or photophores show striking convergences in their structural configurations, biochemical and physiological differences point to many independent evolutionary origins. However, systems capable of flashing all exhibit similar strategies, in contrast to luminous bacteria, which glow continuously. Bacteria frequently are cultivated as symbionts by higher organisms, which then exhibit the same strategies as self-luminous organisms, and may have been the initial source of light in tunicate systems, which exhibit bacterial-like components but flashing behavior in response to stimulation. Similarities and differences among luminous systems are described, with coelenterates, fireflies, marine annelids, and dinoflagellates providing specific examples, in addition to tunicates and bacteria.

240. Hastings, J. Woodland, Hellmuth Broda and Carl H. Johnson (1985). Phase and Period Effects of Physical and Chemical Factors. Do Cells Communicate? In *Temporal Order*, L. Rensing and N. I. Jaeger, eds., New York: Springer-Verlag, pp. 213-221 (also in *Synergetics* (Berlin) 29:213-221).

A temperature compensating mechanism maintains circadian rhythm stability in *Gonyaulax* when environmental temperature changes. Membrane mobility altering chemicals do not affect the period. Light pulses, however, are very effective in phase shifting, as are inhibitors of protein synthesis and certain amino acid analogs. Mixed asynchronous populations maintain their original rhythm for about 2 weeks, but then gradually merge into a single phase. This merger may be prevented by frequent changes of the medium.

241. Hastings, J. Woodland, Hellmuth Broda, Walter Taylor, Jay C. Dunlap and Richard Krasnow (1983). The Mechanism of the Endogenous Cellular Circadian Clock in Relation to 80s Ribosome Protein Synthesis. *Endocytobiology* II.

**ABSTRACT.** Evidence supports the hypothesis that protein synthesis on the 80s ribosome but not the 70s ribosome is essential for proper functioning of

the circadian clock in *Gonyaulax*. Short pulses of protein synthesis inhibitors specific for protein synthesis on the 80s ribosome cause large phase shifts. Even apparent arrhythmia may be induced by proper timing of the pulse.

242. Hastings, J. Woodland and Jay C. Dunlap (1986). Cell-Free Components in Dinoflagellate Bioluminescence. The Particulate Activity: Scintillons; The Soluble Components: Luciferase, Luciferin and Luciferin-binding Protein. In *Bioluminescence and Chemiluminescence Part B*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 307-327 (*Methods Enzymol.* 133:307-327).

Particulate bodies, called scintillons, that possess the potential for bioluminescence can be isolated from *Gonyaulax polyedra* cells. Luciferin, luciferase and luciferin-binding proteins are found both in these bodies and in soluble fraction extracts of *Gonyaulax*. Isolation, purification and assay techniques and chemical and physical properties for scintillons, luciferase, luciferin, and luciferin-binding protein are described. Differences between *Gonyaulax* and other dinoflagellate species are mentioned.

243. Hastings, J. Woodland, Jay C. Dunlap, Elisha Haas, William Vetterling and Richard Krasnow (1980). Single Cell and Population Measurements of Circadian Bioluminescence in *Gonyaulax*. *Eur. J. Cell Biol.* 22(1):495.

**ABSTRACT.** Collisions between cells or between a cell and the container wall do not contribute to spontaneous flashing in *Gonyaulax* nor do the cells flash in response to light. Successive flashes are not correlated in time. The amount of light spontaneously emitted in flashing is not related to the amount emitted in glow. Spontaneous flashing and stimulated luminescence peaks coincide and occur about 2.5 hours into scotophase, while the glow peak occurs at about 10.5 hours, on a 12:12 light-dark cycle. Individual cells flash on the average once per day and show a glow peak similar to that of the population as a whole. However, not all cells either glow or flash, while some flash up to five times.

244. Hastings, J. Woodland and Richard Krasnow (1981). Temporal Regulation in the Individual *Gonyaulax* Cell. In *International Cell Biology 1980-1981*, H. G. Schweiger, ed., New York: Springer-Verlag, pp. 815-822.

Cell division and bioluminescence in *Gonyaulax* are used to measure qualitatively different individual cell behavior in a population, as a step toward understanding timing of physiological functions. In cell division, not all cells divide during division rounds, but all that do divide only at a specific time. In bioluminescence, there is no cooperativity in spontaneous flashing, i.e., flashing frequency per cell is not related to cell number. Likewise, glow intensity per cell and the time of occurrence of the peak are independent of cell number density. Spontaneous flashing and glow also appear to be independent of each other. Continuous flow techniques for measuring luminescent capacity are considerable improvements over aliquot techniques. Individual cell behavior shows great deviations from population averages.

245. Hastings, J. Woodland and John C. Makemson (1983). Iron Represses Bioluminescence in *Vibrio harveyi*: Evidence that the Bioluminescent System has a Metabolic Function. *Abstr., 15th Pacific Science Cong.* 1:97.

**ABSTRACT.** Bioluminescence and luciferase synthesis in the marine bacterium *Vibrio harveyi* are inhibited by iron. Glucose causes further inhibition, but without iron has only a small, transient effect. cAMP does not reverse iron inhibition or glucose inhibition in the presence of iron, but does reverse glucose inhibition in the absence of iron. These findings suggest survival value for the bacteria in low iron, low oxygen conditions.

246. Hastings, J. Woodland, John C. Makemson and Paul V. Dunlap (1987). How Are Growth and Luminescence Regulated Independently in Exosymbionts? *Abstr., 1st Eilat Symp. Marine Symbiosis*.

**ABSTRACT.** Teleost fishes with symbiotic luminous bacteria maintain the bacteria in dense cultures in photophores with low growth rates but bright, continuous bioluminescence. Limitations of iron and/or oxygen and control of osmolarity may achieve this effect, but whether or how the host fish actually controls these postulated factors is not known.

247. Hastings, J. Woodland, John C. Makemson and Paul V. Dunlap (1987). How are Growth and Luminescence Regulated Independently in Light Organ Symbionts? *Symbiosis* 4:3-24.

A key feature in symbiotic mutualisms is the establishment of some sort of equilibrium between host and symbiont, especially with regard to their relative growth rates. Although the imposition of host restriction of symbiont growth would seem simple enough, the contribution(s) provided to the host by the symbiont should presumably not be restricted. Symbioses involving light organs in teleost fishes model the problem elegantly: pure cultures of luminous bacteria are maintained in the organ at a high cell density where growth rate is slow, but luminescence is continuous and intense. How is it possible to constrain growth so severely yet maintain maximal light emission? Studies of growth and luminescence as related to culture conditions have been made for four different species of luminous bacteria, three of which occur in light organs of different fish species. Nutrient limitation may restrict both growth and the development of luminescence, but the latter may be subject to a specific stimulation. In media with low oxygen or low iron, cells grow slowly, but in some species may be intensely luminescent, with a high luciferase content and light emission per cell. Differential effects on growth and luminescence are also related to the osmolarity of the medium in some species. Host regulation of these (and possible other) factors could explain the physiological control of growth and luminescence of symbionts, but no information is available concerning whether or not, and if so how, these postulated factors are controlled within light organs. Since all light organs communicate with the exterior, the infection by the symbiont strain may be postulated to occur from the outside by way of that channel. Since factors responsible for physiological control of growth and luminescence in light organs may be idiosyncratic to a particular species or strain, host control of such factors can in principle contribute to the development and maintenance of a pure culture.

248. Hastings, J. Woodland and Kenneth H. Nealson (1980). Exosymbiotic Luminous Bacteria Occurring in Luminous Organs of Higher Animals. In *Endocytobiology, Endosymbiosis and Cell Biology*, Vol. 1. W. Schwemmler and H. E. A. Schenk, eds., New York: Walter de Gruyter and Co., pp. 467-471.

Luminous bacteria cultured from fish organs all belong to the genus *Photobacterium* and are species-specific for a given host. Bacteria (as yet unidentified) have also been cultured from the

luminous organs of some squid, and bacterial luciferase has been identified in some fish and squid from whose light organs bacteria could not be cultured. In the light organ, the bacteria receive nutrients and a protected environment from the host. The host receives light which it uses for a variety of biological functions and controls via some specific mechanism such as a shutter or chromatophores. Within the light organs unusual, large mitochondria-containing cells have been found which may be involved in regulation of oxygen tension and/or utilization of bacterial excretion products such as pyruvate for energy generation.

249. Hastings, J. Woodland and Kenneth H. Nealson, (1981). The Symbiotic Luminous Bacteria. In *The Prokaryotes: A Handbook on Habitats, Isolation, and Identification of Bacteria*, Mortimer P. Starr, Heinz Stolp, Hans G. Trüper, Albert Ballows and Hans G. Schlegel, eds., New York: Springer-Verlag, pp. 1332-1345.

Luminous bacteria of the genus *Beneckea* may be distinguished from those of the genus *Photobacterium* solely by the speed of decay of their aldehyde-stimulated bioluminescence in vitro. Other specific differences are in the autoinduction of luciferase synthesis, catabolic repression of luciferase synthesis, the effect of oxygen on luminescence emission and nutritional requirements and sugar metabolism. Free-living in the ocean, different species exhibit geographic, seasonal and depth distributions. The mode of living and habitats occupied by luminous bacteria are tabulated. Parasitism, commensalism in the gut of marine animals and symbiosis in fish, squid and possibly tunicate light organs are discussed and the teleost hosts of common luminous bacterial species are charted. Nonmarine luminous bacteria and their habitats are described and the genus *Xenorhabdus* is identified. Techniques for isolating luminous bacteria are outlined.

250. Hastings, J. Woodland, Marie-Thérèse Nicolas and Carl H. Johnson (1985). Subcellular Localization of Substrate (by Fluorescence) and Enzyme (Antibody) Components of the Bioluminescence System of the Unicell *Gonyaulax*. *Abstr., Int. Soc. for Chronobiology, 17th Int. Conf.*

**ABSTRACT.** Bioluminescence flashes in *Gonyaulax* originate from subcellular loci which co-localize with particles in the cell cortex that exhibit

endogenous fluorescence. A luciferase-antiluciferase immune reaction followed by immunogold labeling showed that luciferase localizes on the same particles. The amounts of both luciferin and luciferase exhibit circadian rhythms.

251. Hastings, J. Woodland, Catherine J. Potrikus, Subhash C. Gupta, Manfred Kurfürst and John C. Makemson (1985). Biochemistry and Physiology of Bioluminescent Bacteria. *Adv. Microb. Physiol.* 12:235-291.

The confused taxonomy of luminous marine bacteria is reviewed historically and a classification into three genera, *Vibrio*, *Photobacterium* and *Alteromonas* accepted. *P. fischeri* is reassigned to *Vibrio*, along with all *Beneckea*, and *P. belozerskii* is reassigned to *V. harveyi*. The discovery of a luminous terrestrial bacterial species is documented and designated *Xenorhabdus luminescens*. Bacterial luciferase, its chemical and physical characteristics and its biochemical functions are described and the pathway of its light-producing reaction is pictured. Theories regarding the identity of the light-emitting molecule are analyzed. The possibilities of coupling with FMN<sub>2</sub>-producing enzyme systems is discussed. Purification techniques and the amino acid sequence of luciferase and its subunit structure are presented. The role of aldehydes in the reaction is explained. Models for genetic control of luciferase synthesis are discussed, along with bacterial physiology related to light emission and inhibition mechanisms. Possible ecological roles are outlined. Analytical and clinical applications are suggested.

252. Hastings, J. Woodland, Till Roenneberg and Hellmuth Broda (1985). Medium-Mediated Effects on the Phase and Period of the *Gonyaulax* Bioluminescence Rhythm. *Abstr., Int. Soc. Chronobiology, 17th Int. Conf.*

**ABSTRACT.** After 5-8 days in constant conditions bioluminescence peaks of mixed populations of *Gonyaulax* originally in different phases merged. Unmixed control cultures and mixed cultures in which the medium was changed every two days continued out of phase. These findings suggest cellular communication via the medium.

253. Hastings, J. Woodland, Edward G. Ruby and E. P. Greenberg (1982). The Discrete Vertical Distribution of a Luminous Bacterium in Oceanic

Waters. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 274-278.

Luminous bacteria are reported isolated from oceanic waters overlying the Puerto Rico Trench. *Beneckea* species are found predominately in the upper 150 m of the water column. *Photobacterium phosphoreum* is found only below 200 m and at greatest abundance between 600 and 700 m. Only *P. phosphoreum* is found between 4000 and 7000 m. The total number of isolates steadily decreases with increasing depth. *P. phosphoreum* is probably the exclusive luminous symbiont with luminous fish living at these depths.

254. Hastings, J. Woodland, Walter Taylor, Jay C. Dunlap, Richard Krasnow and Hellmuth Broda (1983). Pulses of Protein Synthesis Inhibitors Phase Shift the Circadian Clock of Bioluminescence in the Marine Dinoflagellate *Gonyaulax*. *Abstr., 15th Pacific Science Cong.* 1:97.

**ABSTRACT.** Evidence supports the hypothesis that protein synthesis on the 80s ribosome but not the 70s ribosome is essential for proper functioning of the circadian clock in *Gonyaulax*. Short pulses of protein synthesis inhibitors specific for protein synthesis on the 80s ribosome cause large phase shifts. Even apparent arrhythmia may be induced by proper timing of the pulse.

255. Hastings, J. Woodland and Shiao-Chun Tu (1981). Bioluminescence of Bacterial Luciferase. *Ann. New York Acad. Sci.* 366:315-327.

The light-producing reaction in luminous bacteria and reaction kinetics and specific activities are presented. The emission maximum and type of display of bacteria are compared to those of dinoflagellates, coelenterates and fireflies. Biophysical and biochemical properties of bacterial luciferase are given and differences between immobilized and nonimmobilized luciferases are described. The structure of the luciferase is described. Spectral differences are discussed. The nature of the emitting species is explored.

256. Hastings, J. Woodland and Shimon Ulitzur (1979). Autoinduction in Luminous Bacteria: A Confirmation of the Hypothesis. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 67.

**ABSTRACT.** By continuous subculturing into fresh medium and dialysis, *Benickea harveyi* has been grown under conditions in which a hypothesized autoinducer molecule for luciferase synthesis cannot accumulate. In these conditions almost no luciferase synthesis occurs, as predicted by the model. Thus the autoinduction hypothesis is confirmed.

257. Haygood, Margo G. (1984). Iron Regulation of Luminescence: Implications for the Ecology and Symbiotic Associations of the Luminous Bacteria. Ph.D. Dissertation, University of California, San Diego.

Bacterial growth rates in the light organs of three fishes, *Monocentris japonicus*, *Kryptophaneron alfredi*, and *Photoblepharon palpebratus* were estimated by rate of release into sterile seawater and found to be 10- to 100-fold repressed relative to laboratory culture. Of the nutrients studied (carbon, nitrogen, phosphorus and iron), limitation of iron had the least deleterious effect on the luminescence. Iron also repressed luciferase synthesis in *Vibrio fischeri*, *Photobacterium phosphoreum*, and *P. leiognathi*. Two models are proposed: iron regulates autoinducer transport or iron acts through an independent repressor system. It is further proposed that luminescence under iron starvation conditions (normal in the marine environment) serves the physiological function of maintaining redox balance while permitting the tricarboxylic acid cycle to function but avoiding loss of carbon by organic acid excretion.

258. Haygood, Margo G. and Daniel H. Cohn (1987). Symbiosis between Anomalopid (Flashlight) Fishes and Luminous Bacteria. *Zool. Sci. (Tokyo)* 4(6):1133.

**ABSTRACT.** DNA extracted from the unculturable luminous bacteroid symbiont found in the light organs of *Kryptophaneron alfredi* shows stronger homology to the luciferase genes of *Vibrio harveyi* than to those of *V. fischeri*. However, differences in codon usage suggest that the symbiont may have acquired the luciferase gene by lateral gene transfer.

259. Haygood, Margo G. and Kenneth H. Nealson (1984). Effects of Iron on Bacterial Growth and Bioluminescence: Ecological Implications. In *Current Perspectives in Microbial Ecology*, J. J. Klug and C. A. Reddy, eds., Washington (D.C.): American Society of Microbiology, pp. 56-61.

Geographic distribution and preferred temperature habitats of various species of luminous marine bacteria are discussed. Symbioses are categorized as relatively non-species-specific enteric symbioses or highly species-specific light organ symbioses. It is observed that the temperature preferences of the bacteria correlate broadly with the temperature habitats of their fish hosts. The physiology of the *Vibrio fischeri*/*Monocentris japonicus* symbiosis is discussed in detail as representative in principle, if not in detail, of bacteria/fish symbioses in general. In this symbiosis, the mechanism of light organ infection is unknown (three theories are presented), but maintenance of the symbiosis involves minimizing bacterial growth while maximizing light output. This balance may be accomplished through autoinduction, catabolite or iron repression, oxygen limitation, or low osmolarity. Evidence is presented to suggest iron repression as the mechanism actually used. Future promising areas of research are suggested.

260. Haygood, Margo S. and Kenneth H. Nealson (1985). Mechanisms of Iron Regulation of Luminescence in *Vibrio fischeri*. *J. Bacteriol.* 162 (1):209-216.

Synthesis of luciferase (an autoinducible enzyme) is repressed by iron in the symbiotic bioluminescent bacterium *Vibrio fischeri*. Possible mechanisms of iron regulation of luciferase synthesis were tested with *V. fischeri* and with *Escherichia coli* clones containing plasmids carrying *V. fischeri* luminescence genes. Experiments were conducted in complete medium with and without the synthetic iron chelator ethylenediamine-di(o-hydroxyphenyl acetic acid). Comparison of the effect of ethylenediamine-di(o-hydroxyphenyl acetic acid) and another growth inhibitor, (2-n-heptyl-4-hydroxyquinoline-N-oxide), showed that iron repression is not due to inhibition of growth. A quantitative bioassay for autoinducer was developed with *E. coli* HB101 containing pJE411, a plasmid carrying *V. fischeri* luminescence genes with a transcriptional fusion between *luxI* and *E. coli lacZ*. Bioassay experiments showed no effect of iron on either autoinducer activity or production (before induction) or transcription of the *lux* operon. Ethylenediamine-di(o-hydroxyphenyl acetic acid) did not affect luciferase induction in *E. coli* strains with wild-type iron assimilation (ED8654) or impaired iron assimilation (RW193) bearing pJE202 (a plasmid with

functional *V. fischeri lux* genes), suggesting that the genes responsible for the iron effect are missing or substituted in these clones. Two models are consistent with the data: iron represses autoinducer transport and iron acts through an autoinduction-independent regulatory system (e.g., an iron repressor).

261. Haygood, Margo G. and Kenneth H. Nealson (1985). The Effect of Iron on the Growth and Luminescence of the Symbiotic Bacterium *Vibrio fischeri*. *Symbiosis* 1:39-51.

Light organs of the marine fish *Monocentris japonicus* contain the luminous bacterium *Vibrio fischeri* in a repressed state of growth. Since the luminescence system of the bacteria is inducible, the environment within the light organ must both promote luminescence and repress growth. Several types of nutrient limitation were tested as candidates for a growth repression mechanism by measuring their effects on luminescence of *V. fischeri* in culture. Cultures limited for C, N and P lost their luminescence; in contrast iron limitation had relatively little detrimental effect on luminescence. Luminescence and the effects of iron on growth and luminescence were tested in liquid and on solid media by addition of ferric ammonium citrate to minimal medium and chelation of iron by ethylenediamine-di (o-hydroxyphenyl acetic acid), EDDA. Synthesis of luciferase was repressed by iron, thus low iron is optimal for luminescence and iron limitation is well suited as a means of growth repression in *M. japonicus* light organs.

262. Haygood, Margo G., Bradley M. Tebo and Kenneth H. Nealson (1984). Luminous Bacteria of a Monocentrid Fish (*Monocentris japonicus*) and Two Anomalopid Fishes (*Photoblepharon palpebratus* and *Kryptophanaron alfredi*): Population Sizes and Growth within the Light Organs and Rates of Release into the Seawater. *Mar. Biol.* 78:249-254.

The light organs of monocentrid and anomalopid fishes consist of bacteria-filled tubular invaginations of the epidermis which are connected to the surrounding seawater by ducts. Bacteria were released from the light organs to estimate bacterial rates of growth in the light organs. For one monocentrid fish (four specimens of *Monocentris japonicus* collected at Jogashima, Japan in 1980) and for two anomalopid fishes (two specimens each of *Photoblepharon palpebratus* collected at Sebu, Philippines in 1981 and

Grand Comore Island in 1975 and *Kryptophanaron alfredi* collected at Parguera, Puerto Rico in 1982), rates of release of bacteria into the surrounding seawater and the bacterial population sizes in the light organs were measured. From this information doubling times of bacteria in the light organs were calculated. In addition, the luminescence of bacteria after their release into the seawater was determined. For *M. japonicus*, two specimens released  $1.1$  to  $6 \times 10^6$  and  $2 \times 10^7$  bacteria  $h^{-1}$ , respectively; the light organs contained about  $1.5 \times 10^8$  bacteria. For *P. palpebratus*, one specimen released  $2.2 \times 10^8$  bacteria  $h^{-1}$ ; a second specimen had light organs containing  $5.2 \times 10^9$  bacteria. For *K. alfredi*, one specimen released  $7 \times 10^7$  bacteria  $h^{-1}$  and had light organs containing  $5.6 \times 10^8$  bacteria; a second specimen released  $3.6 \times 10^7$  bacteria  $h^{-1}$  and had light organs containing  $7.3 \times 10^8$  bacteria. Bacterial doubling times in the light organs of these three fishes were variable and ranged from 7.5 to 135 h in *M. japonicus* and 8 to 23 h in the anomalopids. Bacteria released from *M. japonicus* into the seawater remained viable, but bacteria from all of the fishes soon ceased to emit light.

263. Herrera, Albert A. (1979). Electrophysiology of Bioluminescent Excitable Epithelial Cells in a Polynoid Polychaete Worm. *J. Comp. Physiol.* A129(1):67-78.

An electrophysiological study was made of the bioluminescent epithelial cells (photocytes) of the worm *Hesperonoe complanata* (Polychaeta: Polynoidae). Resting photocyte membrane potential is  $-72 \pm 2$  (s.d.) mV and decreases by 55 mV as external K concentration is increased from 10 to 100 mM. Depolarization activates two separate regenerative inward currents, both resulting in all-or-none action potentials. The action potential with the lower threshold has an amplitude of  $43 \pm 4$  (s.d.) mV, is Na dependent but tetrodotoxin-insensitive and is not associated with luminescence. The action potential with the higher threshold overshoots the reference potential by  $13 \pm 6$  (s.d.) mV, increases by 29 mV for a tenfold increase in Ca concentration and persists in Na-free solution. Under some conditions this spike is followed by a low conductance, Ca-dependent depolarized plateau which abruptly terminates after  $274 \pm 17$  (s.d.) s. Luminescence accompanies each Ca spike. Reducing Ca influx reduces light emission. Depolarization in Ca-free medium does not produce light. It is therefore concluded that the intracellular

light producing mechanism is Ca-activated and that Ca ions mediate excitation-luminescence coupling. Photocytes receive direct excitatory innervation. Large depolarizing postsynaptic potentials occur upon nerve stimulation. These electrical properties adequately explain in vivo bioluminescence.

264. Herring, Peter J. (1978). Bioluminescence of Invertebrates Other Than Insects. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 199-240.

A survey of bioluminescent animals is provided, classified according to phyla and class. Marine groups include radiolaria, sponges, hydrozoans, scyphozoans, anthozoans, ctenophores, nemertines, gastropods, bivalves, cephalopods, polychaetes, pycnogonids, ostracods, copepods, mysids, euphausiids, amphipods, decapods, hemichordates, ophiuroids, asteroids, holothuroids, crinoids, larvaceans and thaliaceans.

265. Herring, Peter J. (1978). Appendix: A Classification of Luminous Organisms. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 461-476.

This article is a list of genera containing luminous species arranged in a taxonomic framework. Doubtfully luminous genera are included and identified.

266. Herring, Peter J. (1979). Some Features of the Bioluminescence of the Radiolarian *Thalassicolla* sp. *Mar. Biol.* 53:213-216.

The luminescence of the solitary radiolarian *Thalassicolla* sp. has a spectral emission maximum at  $440 \pm 4$  nm and the luminescence of crude homogenates can be activated by calcium ions. Electrical stimulation of single individuals frequently causes them to produce repetitive post-stimulus flashing akin to that reported in a number of other marine animals. The possible relationships between the luminescent system of *Thalassicolla* sp. and of certain coelenterates are discussed.

267. Herring, Peter J. (1981). The Comparative Morphology of Hepatic Photophores in Decapod Crustacea. *J. Mar. Biol. Assoc. UK* 61:723-737.

The hepatic photophores of species of *Sergestes* (organs of Pesta) contain fluorescent paracrystalline platelets which are the sources of the luminescence. The cells containing these crystals are contiguous with

cells filled with lipid droplets which act as a diffuse reflector. The optical properties of the organ as a whole derive from the different arrangement of the various regions in the mosaic of individual tubules. The hepatic photophores of *Parapandalus*, *Thalassocaris* and *Chlorotocoides* have a similar anatomical position but differ considerably in structure. They do not contain paracrystalline material and they have a diffuse reflector, probably not composed of lipid, which is separated from the tubules that make up the photocytes. The organs in *Thalassocaris* and *Chlorotocoides* are very similar in structure. Luminescence in the photophores of all four genera is probably intracellular.

268. Herring, Peter J. (1981). Red Fluorescence of Fish and Cephalopod Photophores. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 527-530.

Red fluorescence characterizes the photophores of fish of the genera *Pachystomias*, *Aristostomias*, *Malacosteus*, *Ichthyococcus*, *Polymetme* and *Valenciennellus* and squid of the genus *Histioteuthis*. The chemical nature of the fluorescing molecule is different for each species, but is basically a chromo-protein located in the B cells at the aperture of the photophore. In *Aristostomias* and *Malacosteus* the molecule lacks a porphyrin prosthetic group. In *Histioteuthis* it has the characteristics of a free porphyrin. In most species the light emitted from intact photophores is blue, and the red fluorescent pigment may act as a narrow bandpass blue filter to allow the animal to match the spectrum of downwelling ambient light more exactly. However, the three genera with red fluorescent suborbital light organs emit red light from these organs, but blue light from their postorbital organs. In these fish the red fluorescent molecule appears to act as a secondary emitter in a manner analogous to the green fluorescent protein of *Renilla*.

269. Herring, Peter J. (1981). Studies on Bioluminescent Marine Amphipods. *J. Mar. Biol. Assoc. UK* 61:161-176.

The luminescence of a number of amphipods of the genera *Scina*, *Paraprone*, *Cyphocaris*, *Megalanceola*, *Thoriella* and *Chevreuxiella/Danaella* is described. The flashes of *Scina* spp. are rapid.

80-300 msec in duration, and may be elicited repetitively by electrical stimuli. Cholinesterase inhibitors are potent inducers of luminescence both in whole animals and in isolated appendages. A characteristic postural response is usually associated with mechanically induced luminescence of the larger species of *Sciaenidae*. *Cyphocaryx* and *Chevreauxiella/Danaella* species also respond to electrical stimuli but the luminous responses are of longer duration than those of *Sciaenidae* and are not stimulated by eserine sulphate. In *Parapromoe* luminescence can be most easily induced with dilute hydrogen peroxide and the photogenic cells are associated with a brown pigmented area restricting the light output to a ventral direction. Secretory luminescence has been observed only in *Megalanceola*. It is concluded from the position of the photocytes on the distal regions of the body of all species except *Parapromoe* that luminescence has a primarily deterrent role.

270. Herring, Peter J. (1982). Aspects of the Bioluminescence of Fishes. *Oceanogr. Mar. Biol. Ann. Rev.* 20:415-470.

The literature, generally since 1960, dealing with bioluminescence in fishes is reviewed. Four topics are especially considered: the involvement of luminous bacterial symbionts; the nature and origin of the luminescent system in those fishes not utilizing bacterial symbionts; the neural control of luminescence; and the special control implied by the concept of ventral counterillumination.

271. Herring, Peter J. (1983). The Spectral Characteristics of Luminous Marine Organisms. *Proc. R. Soc. Lond.* B220:183-217.

Measurements of the bioluminescent emission spectra of a wide range of marine animals demonstrate considerable differences between taxa in both the position of the peak emission and the half bandwidth. Although most of the measured spectra are unimodal, some species have either two peaks or one main peak with subsidiary shoulders. Such structured emission spectra are present in several systematic groups and in some cases the emission characteristics have been observed to vary with time. The emission maxima of most species fall within the range 450-490 nm, though maxima from 395-545 nm have been recorded. Species found in the pelagic environment are mostly blue emitting but there is some indication of a relative

increase in green emitting species in the benthic environment. Terrestrial organisms are predominantly yellow-green luminescent. The ecological value of the observed spectral differences is discussed. While the characteristics of the emission spectra have considerable adaptive value for certain functions, some minor spectral variations may not be of ecological significance. Selection for increased quantum efficiency of the luminescence may sometimes predominate over spectral considerations.

272. Herring, Peter J. (1983). Speculations on the Colours of Marine Bioluminescence. *Abstr. 15th Pacific Science Cong.* 1:104.

**ABSTRACT.** Known luminescence emission spectra have maxima ranging from 400-540 nm, with the majority between 455-495 nm, corresponding to the wavelengths for maximum transmission in oceanic waters. When organisms emit outside this window, support for an adaptive value of the unusual spectra is given by the presence of modifying filters or reflectors. Where accessory structures or pigments are lacking, adaptive value is less clear. It is suggested that the spectra in these cases may be determined by biophysical properties inherent in the reaction system.

273. Herring, Peter J. (1984). Lights in the Night Sea. *New Scientist* 101:45-48.

The distribution of luminescence among marine taxa and luminous displays along beaches at night and at sea are described. Luminescence in dinoflagellates is discussed in detail in connection with the luminous bays in Jamaica and Puerto Rico and theories regarding its biological function are presented. Possible functions for bioluminescence in higher marine organisms are also discussed. The mechanisms of the light production are briefly outlined and the structures of several luciferins are pictured. A typical photophore is dissected and depicted. "Milky seas" and "phosphorescent wheels" are described, along with theories of their causes. Interspecific light-producing chemical cross-reactions are documented. Applications to fisheries are mentioned.

274. Herring, Peter J. (1985). Bioluminescence in the Crustacea. *J. Crustacean Biol.* 5(4):551-573.

The taxonomic distribution of bioluminescence among crustaceans is discussed. The contribution of luminous bacteria, whether in photophores or through infections, is mentioned. Photophore patterns, light

intensity and spectra, luminescent behavior, physiology and physicochemical aspects of light production are given. The contribution of crustaceans to the bioluminescence field of the ocean is discussed.

275. Herring, Peter J. (1985). Morphological Variety in Copepod Luminous Glands. *EOS* 66(51):1298.

**ABSTRACT.** Depending on family, luminous glands in copepods are present on the swimming legs, the cephalothorax and abdomen, or both. All open to the sea through pores and eject luminous material in discrete packages. The fluorescent characteristics of the secretion vary with species. One species, *Oncaea conifera*, differs from the others in that its luminous glands open into narrow internal channels rather than to the exterior.

276. Herring, Peter J. (1985). How to Survive in the Dark: Bioluminescence in the Deep Sea. In *Physiological Adaptations of Marine Animals*, M. S. Laverack, ed., Society for Experimental Biology, Cambridge, U.K., pp. 323-350 (*Soc. Exp. Biol. Symp.* 39:323-350).

Bioluminescent tissues in marine organisms may take the form of point source emitters, internal or external glandular organs or glands containing bacterial symbionts. In many cases additional accessory optical structures have been evolved to increase the efficiency of emission, to restrict the angular direction, to focus or collimate the light, to alter its spectral distribution or to guide it from the source to a distant point of emission. This variety of structure is matched by a variety of locations of luminous tissues and organs over the body of different animals. The time course, intensity and spectral nature of bioluminescence are equally variable. Information can be encoded in the spatial pattern, time course and spectral characteristics of bioluminescent signals and the recognition of this information depends upon the visual abilities of the target organism. The known characteristics of the bioluminescence of certain marine organisms are compared with those that would be predicted for different functional interpretations. It is probable that each type of bioluminescent signal in deep-sea organisms is but one factor in the suite of activities which make up a particular behavioral pattern.

277. Herring, Peter J. (1987). Systematic Distribution of Bioluminescence in Living Organisms. *J. Bioluminescence Chemiluminescence* 1:147-163.

A list of the genera of living organisms known or believed to contain luminous species is provided in a systematic context. The constraints on the accuracy of such a list and some aspects of the apparent distribution of bioluminescence are discussed. This list revises the one published by Dr. Herring in *Bioluminescence in Action*.

278. Herring, Peter J., Malcolm R. Clarke, S. von Boletzky and K. P. Ryan (1981). The Light Organs of *Sepiolo atlantica* and *Spirula spirula* (Mollusca: Cephalopoda): Bacterial and Intrinsic Systems in the Order Sepioidea. *J. Mar. Biol. Assoc. UK* 61:901-916.

The light organs of *Sepiolo atlantica* and *S. robusta* are embedded within the ink sac and consist of epithelial pockets enclosing large numbers of symbiotic luminous bacteria. The bacteria impart a yellow color to the center of the organ and have been identified as *Photobacterium fischeri*. The bacterial pockets connect with the exterior via a ciliated duct opening at a mediolateral papilla. The intensity of emitted light can be regulated and is increased in response to a brief illumination of the animal. Light is normally emitted continuously and is visible only in ventral view. In *Spirula spirula*, in contrast, there is no indication of any bacterial involvement in light emission. The light organ is a discrete hemisphere of tissue which is highly lamellate in structure though unlike the photocytes of other cephalopods. Beneath it is a reflector of collagen fibrils and dense platelets in the tissues immediately around it provide a diffuse reflectance. In larger specimens similar platelets form a spherical lens-like structure over the photogenic tissue.

279. Herring, Peter J., P. N. Dilly and Celia Cope (1985). The Photophore Morphology of *Selenoteuthis scintillans* Voss and Other Lycoteuthids (Cephalopoda: Lycoteuthidae). *J. Zool. (London)* A206:567-589.

Females and juveniles of *Selenoteuthis scintillans* have photophores of several structural types, distributed on the tentacles and eyeballs, and within the mantle cavity and tail. Three distinct

photophore types can be recognized on the basis of their accessory structures, though their photocytes are identical. The tail and some tentacular photophores (Type 1) lack any accessory optical structures; other tentacular and abdominal photophores (Type 2) have collagenous diffusing fibres; the anal and ocular photophores (Type 3) have a variety of iridosomes but no collagen. The distal tentacular organ is a double structure composed of a unit each of Type 1 and Type 2. Ocular photophores 1 and 5 are also double structures, composed of two Type 3 units. The photophores closely resemble in structure those of *Lycoteuthis diadema*. The photocytes have a marked fluorescence and luminesce on treatment with dilute hydrogen peroxide. The bioluminescence intensity of the tail organ may be modified by chromatophore movements and has a blue-green spectral emission. The photophores of juvenile *Lampadoteuthis megaleia* are similar in structure to those of *Selenoteuthis* but somewhat less complex. A comparison between the morphology of the photophores of lycoteuthid and enoploteuthid squids emphasizes the close similarity between the two families. At the ultrastructural level, certain photophores of both families have very characteristic microvillous blood vessels associated with the photocytes.

280. Herring, Peter J., P. N. Dilly and Celia Cope (1987). The Morphology of the Bioluminescent Tissue of the Cephalopod *Japetella diaphana* (Octopoda: Bolitaenidae). *J. Zool.* (London) 212:245-254.

Maturing females of the octopod *Japetella diaphana* (Hoyle) develop a luminous oral ring. Studies of specimens of different size show that this structure develops from a muscular ring which undergoes great cellular proliferation, associated with gradual degeneration of the original muscle. The light-producing cells (photocytes) have a relatively uniform cytoplasm whose most characteristic components are small mitochondria, granular aggregates and microtubular or microfibrillar bundles. It is concluded that the original muscle tissue is not transformed directly into luminous tissue. Possible uses of the luminescence are discussed, based on the postures adopted by live specimens in shipboard aquaria.

281. Herring, Peter J. and Paul Horsman (1985). Phosphorescent Wheels: Fact or Fiction? *Mar. Obs.* 55:194-201.

Phosphorescent (really bioluminescent) wheels are described, in part by quoting original reports, and their distribution is mapped. Questions concerning the source of the light and its observed patterns and movements are considered. Several theories are presented, compared and criticized.

282. Herring, Peter J. and James G. Morin (1978). Bioluminescence in Fishes. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 273-329.

A comprehensive survey of bioluminescence in fishes is provided.

283. Hickman, G. Daniel (1980). Distribution and Characteristics of Fluorescent and Bioluminescent Matter in the World's Oceans. In *Advanced Concepts in Ocean Measurements for Marine Biology*, Ferdinand P. Diemer, F. John Vernberg and Donna Z. Mirkes, eds., Columbia (South Carolina): University of South Carolina Press, pp. 131-150.

The current status of research concerning the distribution and characteristics of the luminescence (fluorescence/bioluminescence) in the world's oceans is reviewed. One of the goals of this program was to determine the feasibility of (1) using fluorescence techniques to identify and map distributions of chlorophyll, red tides and Gelbstoff; (2) sensing bioluminescence from aircraft and satellites; and (3) using such data as an indirect measure of temperature and salinity. Requirements exist for in situ, laboratory, and remote sensing experiments of each subject category listed. Aircraft remote sensing experiments should be designed and coordinated with extensive ground truth measurements made from ships. Such aircraft experiments should include a variety of optical sensors such as multispectral scanners, low-light-level television and lasers. The results of these aircraft/ground truth programs will provide a sound basis for future laboratory and field measurement programs in luminescence.

284. Hickman, G. Daniel (1980). Laser Induced Luminescence for Measurement of Nearsurface Temperature and Salinity and Laser/Acoustic

Technique for Shallow Turbid Water Bathymetry. Abstracts and Recommendations from the *Bolkesjo Workshop on Remote Measurement of Underwater Parameters*, Royal Norwegian Council for Scientific and Industrial Research, Space Activity Division Report SAD-91-T, pp. 16-18.

**ABSTRACT.** Bioluminescence per se varies little with temperature. However, different luminous organisms, which may be identified by their flash spectral and kinetic characteristics, are found in different bodies of water and may, perhaps, be used to characterize those bodies, including temperature. Experiments regarding temperature dependence of the bioluminescent flash of dinoflagellates stimulated by high energy laser pulses are underway.

285. Hickman, G. Daniel, John A. Edmonds and Richard V. Lynch (1984). Laser-Induced Marine Bioluminescence Measurements and the Potential for Airborne Remote Sensing. *Remote Sensing of Environment* 15:77-89.

Bioluminescence in cultures of the dinoflagellate *Pyrocystis lunula* at various temperatures were stimulated using a pulsed dye laser and Rhodamine 6G dye having an optimum lasing wavelength of  $586 \pm 30$  nm. Following an intense "first flash" response, the flash intensity decayed in logarithmic fashion with successive laser shots. Samples pulsed to exhaustion were found to recover completely during the 12 h photophase. The total stimuable light (TSL) was calculated to be between  $4.5 \times 10^{-10}$  J cell<sup>-1</sup> and  $38.5 \times 10^{-10}$  J cell<sup>-1</sup>. The time from stimulation to maximum light emission ( $t_m$ ) was found to vary with temperature logarithmically from approximately 11°C to 28°C. The corresponding regression equation was found to predict temperatures to within  $\pm 0.4^\circ\text{C}$ . These results provide the basis for predicting the feasibility of an airborne laser transceiver for mapping the distribution of ocean bioluminescence. The potential exists for determining ocean surface/near surface temperature from measurements of the response pulse time parameters.

286. Hickman, G. Daniel, John A. Edmonds, Robert D. Pike, Nicholas Antonoff and Richard V. Lynch (1983). Temperature Dependence of Laser-Induced Bioluminescence in *Pyrocystis lunula*. In *Proceedings of the Los Alamos Conference on Optics '83*, Bellingham, Washington, Society of Photo-Optical Instrumentation Engineers, Vol. 380, pp. 411-414.

Cultures of *Pyrocystis lunula* were stimulated at various temperatures with laser pulses. The time from stimulation to maximum light emission ( $t_m$ ) was found to vary with temperature logarithmically from approximately 11°C to 28°C. The corresponding regression equation was found to predict temperatures to within  $\pm 0.4^\circ\text{C}$ . Beyond this temperature range, "death glow" occurred, during which *P. lunula* did not respond to laser stimulation. These findings suggest a possible means of remotely determining ocean surface temperatures.

287. Hickman, G. Daniel, Bernadette Johnson and Richard V. Lynch (1981). Laser-Induced Bioluminescence of *Pyrocystis lunula*: Its Dependence on Source Wavelength and Intensity. In *Proc., Conf. Laser-Induced Processes in Biological Molecules*, July 6-8, 1981, Stanford University, pp. 140-157.

Reports of stimulation of bioluminescence by light pulses are reviewed. Equipment and techniques for stimulating flashing in the dinoflagellate *Pyrocystis lunula* are described. Flash intensity correlates generally with laser excitation energy, but attempts to observe intensity variations dependent on the excitation wavelength are inconclusive.

288. Hickman, G. Daniel and Richard V. Lynch (1981). Laser-Induced Bioluminescence. In *Proceedings of the Los Alamos Conference on Optics '81*, Bellingham, Washington, Society of Photo-Optical Instrumentation Engineers, Vol. 288, pp. 263-268.

A project was initiated to determine the feasibility of developing a "complete airborne remote sensing system" for rapidly mapping high concentration patches of bioluminescent organisms in the world's oceans. Conceptually, this system would be composed of a laser illuminator to induce bioluminescence and a low light level image intensifier for detection of light. Our initial laboratory measurements consisted of using a 2-J flash lamp pulsed optical dye laser to excite bioluminescence in the marine dinoflagellate *Pyrocystis lunula* at ambient temperature using Rhodamine 6G as the lasing dye (585 nm) and a laser pulse width of 1  $\mu\text{sec}$ . After a latency period of 15-20 msec, the bioluminescence maximum occurred in the blue (480 nm) is the

wavelength maximum for most dinoflagellate bioluminescence) with the peak occurring approximately 65 msec after the laser pulse. Planned experiments will investigate the effect of different excitation wavelengths and energies at various temperatures and salinities of the cultures.

289. Hiller-Adams, Page and James F. Case (1984). Optical Parameters of Euphausiid Eyes as a Function of Habitat Depth. *J. Comp. Physiol.* A154:307-318.

The relationships between habitat depth, eye diameter relative to body length, and the dimensions of rhabdoms and crystalline cones have been examined for 13 species of three oceanic euphausiid genera with habitats ranging from near-surface waters to the deep-sea. Rate of eye growth decreases with depth. Longer rhabdoms may increase the visual sensitivity to point and extended light sources by an eye of a particular size with depth. Larger interommatidial angles suggest that visual acuity decreases with depth. Depth-related changes in euphausiid eyes are considered with respect to the probable roles of vision and bioluminescence in the deep sea. Unusual features of the eyes of several species are described.

290. Hobohm, U., G. Cornelius, Walter Taylor and Ludger Rensing (1984). Is the Circadian Clock of *Gonyaulax* Held Stationary After a Strong Pulse of Anisomycin? *Comp. Biochem. Physiol.* 79A(3):371-378.

*Gonyaulax polyedra* cells were treated with two sequential pulses of a protein synthesis inhibitor (anisomycin) in order to analyze a possible stopping of the circadian clock by the first pulse. Inhibition of protein synthesis during these pulses and after centrifugation and resuspension of the cells was determined by measuring the incorporation of labelled amino acids. The effects of the second pulses on the clock were measured as phase shifts of the glow rhythm with respect to a control rhythm that had been subjected to the initial pulse only. From the observed phase shifts of the second pulses, they conclude that the clock is not stopped by the first pulse but is immediately shifted to a different phase.

291. Hobson, Edmund S., William N. McFarland and James R. Chess (1981). Crepuscular and Nocturnal Activities of Californian Nearshore Fishes, with

Consideration of Their Scotopic Visual Pigments and the Photic Environment. *Fish. Bull.* 79(1):1-30.

Activities in 27 of the major southern Californian nearshore fish species, with emphasis on trophic relationships, were studied between 1972 and 1975 at Santa Catalina Island. Because these fishes orient primarily by vision, they are strongly influenced by the underwater photic environment, which is defined with representative spectra. Crepuscular and nocturnal events are centered upon, but daytime events for comparison are also described. The species that feed mostly by day include *Atherinops affinis*, *Paralabrax clathratus*, *Girella nigricans*, *Medialuna californiensis*, *Brachyistius frenatus*, *Cymatogaster aggregata*, *Damalichthys vacca*, *Embiotoca jacksoni*, *Chromis punctipinnis*, *Hypsypops rubicunda*, *Halichoeres semicinctus*, *Oxjulis californica*, *Semicossyphus pulcher*, *Alloclinus holderi*, *Gibbonsia elegans*, *Heterostichus rostratus* and *Coryphopterus nicholsi*. Those that feed mostly at night include *Scorpaena guttata*, *Sebastes atrovirens*, *S. serranoides* (subadult), *S. serriceps*, *Xenistius californiensis*, *Seriphus politus*, *Umbrina roncadore* and *Hyperprosopon argenteum*. Those that show no clear diurnal or nocturnal mode include *Leiocottus hirundo* and *Pleuronichthys coenosus*. Activity patterns tend to be defined less clearly in the warm-temperate fish communities of California than in fish communities of tropical reefs. Included are the twilight patterns of transition between diurnal and nocturnal modes, which are considered to be defined by predation pressures. The lesser definition of twilight patterns in California could mean reduced crepuscular predation there, but Californian fishes, too, are hypothesized to have evolved under severe threats from crepuscular and nocturnal predators. This is evidenced in the spectral sensitivities of their scotopic visual pigments, which cluster around 500 nm—the best position for vision during twilight and at night in Californian coastal waters. Although the scotopic system dominates vision in dim light, the spectral sensitivities of the scotopic pigments are poorly matched to the major forms of incident light at night—moonlight and starlight. Rather, they match twilight and bioluminescence, which favor similar spectral sensitivities. This is believed to benefit these fishes most on defense. The match with twilight, when the low levels of incident light shift briefly to shorter wavelengths, enhances vision during the crepuscular periods of intensified threats from

predators. And the match with bioluminescence permits fishes to react to threatening moves in nocturnal predators by responding to luminescing plankton that fire in the turbulence generated by these moves.

292. Hoffmann, Birgit and Rüdiger Hardeland (1985). Membrane Fluidization by Propranolol, Tetracaine and 1-Aminoadamantane in the Dinoflagellate, *Gonyaulax polyedra*. *Comp. Biochem. Physiol.* 81C(1):39-43.

In microsomal membranes from *Gonyaulax polyedra*, the fluidity was investigated by means of fluorescence polarization measurements, using 1-anilinonaphthalene-8-sulfonate (ANS), N-phenylnaphthyl-(1)-amine (NPN) and 1, 6-diphenyl-1, 3, 5-hexatriene (DPH) as membrane probes. Membrane fluidity was increased by propranolol, tetracaine and 1-aminoadamantane. The inner, hydrocarbon domains of the membranes were fluidized at considerably lower concentrations of these drugs, as compared to peripheral regions of the lipid bilayer. Effects of these compounds on bioluminescence and on the circadian clock of *Gonyaulax* might be related to the changes in membrane fluidity.

293. Hoffmann, Klaus H. (1981). Leuchtende Tiere: Chemie und Biologische Bedeutung. *Biologie in Unserer Zeit* 11(4):97-106 (German).

A brief table of the taxonomic distribution of bioluminescence among various groups of organisms is provided. The biochemistry and physical chemistry of the light-producing reactions of bacteria, fireflies, coelenterates and dinoflagellates are described and seven mechanisms are charted. The structures of five luciferins are pictured. The morphology and histology of light organs in several organisms are described and pictured. The relation between light emission and vision and other possible biological functions for bioluminescence are explored. The spectral emission peaks and intensity maxima for eight organisms are tabulated.

294. Holderied, Kristine (1984). The Effect of Controlled Pressure Changes on the Stimulation of Bioluminescence in *Pyrocystis lunula*. U.S. Naval Academy, Annapolis, Maryland. Trident Scholar Project Report No. 129.

Bioluminescence in a dinoflagellate species, *Pyrocystis lunula*, was stimulated by controlled,

repeated pressure changes. Pressure pulses of a 2-sec duration were used to determine their effect on stimulated bioluminescence. Observations of organism sensitivity in response to the circadian rhythm, light phase and cell fatigue were also made. The pressure change was effected by valve-regulated compressed air. The luminescence was detected with a photomultiplier tube. The mean threshold for luminescence in *Pyrocystis lunula* was found to be  $5.10 \pm 1.70$  psi. Pressure decreases were found to be much more effective than pressure increases. Three other rates of pressure change were investigated and a rough correlation was established between higher rates of pressure change and slightly lower threshold levels. Qualitative observations indicated that increased rates of pressure change were also associated with higher initial flashes and faster fatigue times. Pulse length appeared not to affect the stimutable luminescence to any significant degree. Measurements made at various times in the scotophase revealed a relatively constant, high level of light output, while only minimal, if any, light output was detected in the photophase. The resulting threshold level was applied to a pressure field model around a submerged cylinder and the probable location of bioluminescence was predicted.

295. Holzman, Thomas F. and Thomas O. Baldwin (1981). Binding of 2,2-Diphenylpropylamine at the Aldehyde Site of Bacterial Luciferase Increases the Affinity of the Reduced Riboflavin 5'-Phosphate Site. *Biochemistry* 20(19):5524-5528.

A new class of inhibitors of the bacterial bioluminescence reaction, the N, N-diphenyl-alkylamines and acids, has been found. The action of one of these compounds, 2,2-diphenylpropylamine is studied. The amine was competitive with the long-chain aliphatic aldehyde substrate ( $K_i = 0.1$  mM) but caused an increase in the affinity of the enzyme for reduced riboflavin 5'-phosphate (FMNH<sub>2</sub>). The inhibitor was attached to Sepharose 6B by a bis(oxirane) spacer, and the interactions of bacterial luciferase with the immobilized ligand were analyzed. The binding of luciferase to the immobilized inhibitor was enhanced by FMNH<sub>2</sub> and was decreased by decanal. The results of these studies showed that the 2, 2-diphenylpropylamine-luciferase complex has an increased affinity for FMNH<sub>2</sub>. Likewise, the FMNH<sub>2</sub>-luciferase complex has an increased affinity for 2,2-diphenylpropylamine. The inhibitor also binds to the enzyme-4a-peroxydihydroflavin complex to

block the binding of the aldehyde substrate, while binding of the aldehyde substrate to either the free enzyme or the enzyme-4a-peroxydihydroflavin complex blocks binding of 2,2-diphenylpropylamine.

296. Holzman, Thomas F. and Thomas O. Baldwin (1983). Reversible Inhibition of the Bacterial Luciferase Catalyzed Bioluminescence Reaction by Aldehyde Substrate: Kinetic Mechanism and Ligand Effects. *Biochemistry* 22:2838-2846.

The bioluminescence reaction catalyzed by bacterial luciferase from the luminous marine bacterium *Vibrio harveyi* was found to be subject to reversible, chain length dependent inhibition by aldehyde substrate. The stoichiometry of aldehyde to luciferase in the bioluminescence reaction was 1:1; the kinetics of substrate inhibition were consistent with the binding of a second molecule of aldehyde to luciferase to form an enzymatically inactive complex. These findings indicated that aldehyde interactions with bacterial luciferase from *V. harveyi* could not be adequately described by simple Michaelis-Menten kinetics. The binding of n-decanal to luciferase and the bioluminescence reaction velocity were dependent on buffer composition and concentration. Phosphate binding to luciferase reduced enzyme affinity for binding a second molecule of aldehyde; the reciprocal effect was also observed. The existence of a reversible complex between the aldehyde substrate and luciferase suggested that the reaction in vitro did not require ordered binding of FMNH<sub>2</sub> and aldehyde, in contrast to the commonly depicted kinetic model implying ordered substrate binding. The data presented here, along with recent observations, suggest a kinetic model for the luciferase-catalyzed reaction in which the order of substrate binding is random.

297. Horii, Naojiro (1982). Observation on Luminous Polychaeta, *Odontosyllis undecimdonga*, from Toyama Bay, Japan Sea. *Sci. Rep't Yokosuka City Mus.* 29:1-3 (Japanese).

It is well known that a luminous swimming polychaete from Bermuda and the Banda islands exhibits a characteristic biorhythm. Recently, the same kind of species (*Odontosyllis undecimdonga* Imajima et Hartmann) was also found to live in Toyama Bay. Early in October in 1975, numerous luminous polychaetes were collected, after sunset, from near the surface of the illuminated coastal water using a portable searchlight at the Uozu seashore in Toyama

Bay. From detailed observations from 1975 to 1981, it became clear that the luminous polychaete appeared for about 0.5 hour about 1 hour after sunset only in a period of approximately 20 days from the beginning to the middle of October in each year.

298. Horsman, Paul V. (1985). *Seawatch. The Seafarer's Guide to Marine Life*. New York: Facts on File.

Chapter 3 of this book provides a brief historical overview of bioluminescence observations at sea. Types of luminous displays are classified and mapped and principal light-producing marine organisms are tabulated along with their distributions. Chemical and bacterial production of light in photophores of higher organisms is briefly mentioned and possible biological functions for light emission are well described.

299. Houbrick, Richard S. (1987). Anatomy, Reproductive Biology, and Phylogeny of the Planaxidae (Cerithiacea: Prosobranchia). *Smithsonian Contrib. Zool.* 445:1-57.

The family Planaxidae Gray comprises a small, monophyletic, mainly pantropical marine group of six extant genera in the superfamily Cerithiacea Fleming that are adapted to an intertidal environment. They are microphagous herbivores and usually occur in large populations on hard substrates. Planaxids are gonochoristic and have open pallial gonoducts, aphilic males, produce spermatophores, and brood their young in specialized cephalic brood pouches of ectodermal origin. Embryos of most species are released at the veliger stage and undergo a planktotrophic phase before settlement, but some species undergo a direct, lecithotrophic development. Species in the genus *Angiola* are unique among prosobranchs in having a bioluminescent mantle organ. On the basis of morphological homology, otogeny, and advocacy, *Batillaria* (of the subfamily Batillariinae, family Potamididae) and *Melanoides* (of the freshwater family Thiaridae) were chosen as outgroups for phylogenetic analysis of all genera except *Holcostoma*. The polarities of characters were established by outgroup comparison, and transformation series of multistate characters were ordered by structural complexity and by reciprocal illumination. Two equally parsimonious cladograms were produced that arrange the taxa in essentially similar sequence. *Planaxis* and *Fissilabia* share many apomorphies as do *Angiola* and *Hinea*. Six recent

genera are recognized as comprising the Planaxidae: *Planaxis* Lamarck, 1822; *Fissilabia* Macgillivray, 1836; *Supplanaxis* Thiele, 1929; *Hinea* Gray, 1847; *Angiola* Dall, 1926; *Holcostoma* H. and A. Adams, 1853. Synonymies, conchological, radular and anatomical descriptions, and the ecology and life histories of each genus are presented.

300. Huber, Michael E., A. Charles Arneson and Mark R. Abbott (1987). Identification of Euphausiid Shrimps from Properties of Their Bioluminescence. *EOS* 68(50):1695.

**ABSTRACT.** A CCD spectrophotometer with a spectral resolution of 4–7 nm and a temporal resolution of 30 msec can distinguish the euphausiids *Nyctiphanes simplex*, *Nematoscelis difficilis* and *Thysanoessa spinifera* from one another on the basis of their bioluminescence emissions. Both spectral and temporal information were useful in discriminating among species, but temporal information was more useful.

301. Huber, Michael E., A. Charles Arneson, Kenneth H. Nealson and Mark R. Abbott (1985). Discriminant Analysis of Spectral and Kinetic Properties of Marine Bioluminescence. *EOS* 66(51):1321.

**ABSTRACT.** Discriminant analysis based on the flash kinetic parameters of rise time, decay time and total time and the emission spectral ratios of light intensities at 480 and 520 nm to the intensity at 500 nm could successfully distinguish among 10 different luminous marine organisms. Rise time and decay time alone gave 83.1% correct species classification, while spectral analysis alone gave only 77.5% success. All four properties together gave 100% classification success.

302. Hughes, Bryn C. (1984/85). An Investigation into Fluorescence and Bioluminescence in Laboratory Culture of Phytoplankton found in the North Atlantic. Bristol Polytechnic Report, Research Agreement #2192/02 AMTE 8.

Visual sightings of bioluminescence by merchant and Royal Navy vessels reported to the Hydrographic Department, Taunton, between 1981 and 1984 are summarized. Bioluminescence and related data gathered on cruises in four areas of the Atlantic are reported along with taxonomic identifications and organism counts to determine probable causative

organisms. A survey of instrumental measuring systems is presented.

303. Inoue, Shoji, Hisae Kakoi, Mikiko Murata, Toshio Goto and Osamu Shimomura (1979). Coelenterate Bioluminescence III. Trace Characterization of Luminescence Substances of *Cavernularia obesa* and *Ptilosarcus guernei*. *Chem. Lett.* 1979:249–252.

Trace amounts of luminescent substances of *Cavernularia obesa* and *Ptilosarcus guernei* were characterized to be *Renilla* luciferin and luciferyl sulfate using 100 g of *C. obesa* in quiescent state and 200 g of *P. guernei* in frozen state.

304. Inoue, Shoji, Hisae Kakoi, Kunisuke Okada and Toshio Goto (1979). Fish Bioluminescence II. Trace Characterization of the Luminescence System of a Myctophina Fish, *Diaphus elucens*. *Chem. Lett.* 79:253–256.

*Oplophorus* luciferin (Ia) was characterized in a pair of nasal photophores of a myctophina fish, *Diaphus elucens*. Liver of the fish contains luciferin in a bound form, possibly as its enol ether. A luciferase active toward *O. luciferin* was extracted from the flesh of the fish. From these results it is concluded that the luminescence system of *D. elucens* is similar to that of *Oplophorus* and not to that of *Cypridina*.

305. Inoue, Shoji, Hisae Kakoi, Kunisuke Okada, Hideo Tanino and Toshio Goto (1983). Trace Characterization of the *Watasenia* Luciferin in Eye and Skin Photophores and in Liver of *Watasenia scintillans*. *Agric. Biol. Chem.* 47(3):635–636.

A possible bioluminescent substrate, *Watasenia* luciferin, previously isolated from the arm photophores of the squid, *Watasenia scintillans*, has also been isolated from the skin, eyes and liver. These results indicate that it is synthesized in the liver and conveyed to the photophores. Recycling after use may also occur. The luciferin structure is shown.

306. Ismailov, A. D., N. A. Baranova, V. S. Danilov and N. S. Egorov (1981). Inhibition of Bacterial Luminescence by Substrates of Cytochrome P-450. *Biochemistry* (USSR) 46(2):234–239 (Russian) :192–196 (English).

The mechanism of luminescence quenching by various drugs (dimethylaniline, ethylmorphine, hexobarbital, and aminopyrine), which are efficient

inhibitors of the luminescence of both intact cells and bacterial luciferase, was investigated. It was found that the inhibition of luminescence occurs through competition with the substrate of the luminescent system of bacteria—an aliphatic aldehyde in cytochrome P-450. It was concluded that the luminescent system of bacteria is similar in a functional respect to the microsomal hydroxylating system.

307. Ismailov, A. D., N. A. Baranova, N. S. Egorov and V. S. Danilov (1980). Electron Transport Systems of *Photobacterium fischeri*. *Microbiology (USSR)* 49(3):377–382 (Russian) :260–264 (English).

We have studied the composition of cytochromes of *Photobacterium fischeri* at different growth phases and under different culturing conditions. Electron transport chains of bacteria investigated are characterized by the presence of cytochromes of the b and c types. The terminal oxidases are cytochromes o,  $a_2 + a_1$ , and P-450. The hemoprotein P-450 functions as a mixed function oxidase. It was shown that the qualitative composition of bacteria does not depend on the growth phase but on the culturing conditions. In the case of oxygen deficiency the bacteria synthesize cytochromes  $a_2 + a_1$ .

308. Ismailov, A. D., V. S. Danilov, Yu. A. Malkov and N. S. Egorov (1981). Inhibitor Analysis of the Luminescent Electron Transport Chain of *Photobacterium fischeri*. *Biochemistry (USSR)* 46(1):40–46 (Russian) :30–35 (English).

The peculiarities of the quenching of the fluorescence of a preparation of bacterial luciferase from *Photobacterium fischeri* by nonspecific electron acceptors and inhibitors of dehydrogenases were investigated. Inhibition of the luminescence reaction occurs according to a noncompetitive mechanism with NADH, FMN, and an aliphatic aldehyde. The inhibitors, in competition with cytochrome c, suppress the NADH-cytochrome c oxidoreductase activity. It was concluded that the most sensitive component of the luminescent electron transport chain is an iron-containing protein—lumiredoxin.

309. Ives, J. David (1987). Possible Mechanisms Underlying Copepod Grazing Responses to Levels of Toxicity in Red Tide Dinoflagellates. *J. Exp. Mar. Biol. Ecol.* 112:131–145.

A previous study indicated that rates of ingestion exhibited by adult female copepods of *Acartia hudsonica* (Pinhey) and *Pseudocalanus* spp. were lowered by increasing levels of toxicity in clonal cultures of the bloom-causing dinoflagellate *Protogonyaulax tamarensis* (Taylor). In the present study, three types of laboratory grazing experiments were performed to determine which of two contending hypotheses—behavioral rejection or physiological incapacitation—could explain the observed relationship best. The experimental results consistently supported the postulated mechanism of physiological incapacitation and not the mechanism of behavioural rejection, as the reason for the lowered rates of ingestion on the more toxic dinoflagellate clones.

310. Jamieson, Barrie G. M. and John E. Wampler (1979). Bioluminescent Australian Earthworms II. Taxonomy and Preliminary Report of Bioluminescence in the Genera *Spenceriella*, *Fletcherodrilus*, and *Pontodrilus* (Megascolecidae:Oligochaeta). *Aust. J. Zool.* 27(4):637–669.

Bioluminescence is demonstrated in four species of *Spenceriella*, in *Fletcherodrilus fasciatus* and *F. unicus*, all being megascolecines from eastern Australia, and in the circummundane megascolecine *Pontodrilus bermudensis*, and is compared with that of the North American acanthodrilid *Diplocardia longa*. The four *Spenceriella* species are placed in a new *cormieri* species-group in the subgenus *Spenceriella*. Of these, *S.(S.) cormieri*, *S.(S.) curtisi* and *S.(S.) noctiluca* are new species and calciferous glands, and the subgenus *S. Austroscolex* is distinguished in lacking buccopharyngeal or other tufted nephridia anteriorly. *Fletcherodrilus* is redefined and a key to its four species provided. The synonymy and world distribution of *Pontodrilus bermudensis* Beddard is given. On electrical or tactile stimulation the seven described species, in *Spenceriella*, *Fletcherodrilus* and *Pontodrilus*, all exhibit spontaneous luminescence which is enhanced by addition of peroxide and which cross reacts with *Diplocardia longa* luciferase and, usually luciferin. It is suggested that the luminescent system resides in the free chloragogen cells (eleocytes) in the coelomic fluid, in all except *P. bermudensis* in which luminescence is not cell bound. Five species studied in the megascolecine genera *Heteropodrilus*, *Spenceriella* (*Austroscolex*) and *Digaster*, and the glossoscolecid *Pontoscolex*

*corethrurus*, are nonluminescent. Possible functions of luminescence are discussed.

311. Jamieson, Barrie G. M., John E. Wampler and Michael C. Schultz (1981). Preliminary Ultrastructural Description of Coelomocytes of the Luminescent Oligochaete, *Pontodrilus bermudensis* (Annelida). In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 543-59.

On strong electrical, mechanical or chemical stimulation the marine littoral earthworm *Pontodrilus bermudensis* exudes a luminous slime with peak emission at 550 nm. Emission may be further stimulated by  $H_2O_2$  and/or *Diplocardia longa* luciferase, which result suggests that *Pontodrilus* luciferin is n-iso-valeryl-3-amino-propanal or a close analog. The slime contains cells identical with coelomocytes in *Diplocardia*, which are classified into nine types and described in this report. Of these types, the mucocyte cells are the most likely source of the bioluminescence, but lobopodial granulocytes or a combination of two or more cell types cannot be ruled out.

312. Janssen, John and G. R. Harbison (1985). Diagonally Descending Hatchetfish Swim with the Body Horizontally Oriented. *EOS* 66(51):1264.

**ABSTRACT.** Observations during a descent on the submersible Johnson-Sea-Link II showed that the hatchetfish *Argyrolepecus* did not tilt its body while descending. This unusual swimming behavior keeps its photophores pointed downward and its telescopic eye pointed upward and may be made possible by the odd body shape and skeletal and muscular peculiarities. This behavior lends support to the countershading theory of bioluminescence function.

313. Janssen, John, G. R. Harbison and J. E. Craddock (1986). Hatchetfishes Hold Horizontal Attitudes during Diagonal Descents. *J. Mar. Biol. Assoc. UK* 66:825-33.

Based on analysis of videotape records, species of the genus *Argyrolepecus* are capable of swimming diagonally downward at considerable speeds without altering their body postures. Morphological evidence strongly suggests that they are able to swim diagonally upwards in a similar way. Their distinctive hatchet-like profile presents a streamlined airfoil in both

diagonal and horizontal movements, even though the body is not tilted. Modifications of the caudal musculature probably enable all hatchetfishes (including members of the other two genera, *Polyipnus* and *Sternoptyx*) to use the tail for propulsion for both diagonal and horizontal movements. The dorsal fin probably aids in diagonally downward movements and the pelvic and anal fins in diagonally upward movements, whilst the pectoral fins serve as stabilizers for these movements and as an axis of rotation for striking at prey. The seemingly ungainly shape of the hatchetfish is the result of achieving a streamlined, fish-like shape for horizontal and diagonal movements without tilting of the body, presumably in order to maintain an effective camouflage in midwater. In the journal, the title of this article is visually amusing in that the words "Hold Horizontal Attitudes" are all on a straight horizontal line, while the words "during Diagonal Descent" are offset on successive lines, thus forming a pattern like a hatchetfish descending while holding its body horizontal. The use of alliteration is also noted, both the accustomed alliteration of modern poetic practice, and the stressed alliteration and half-line structure of Old English poetry.

314. Jayabalan, N. (1980). Studies on Silver-Bellies (Pisces:Leiognathidae) and Their Associated Bioluminescent Bacteria of Porto Novo Water. Ph.D. Dissertation, Annamalai University, Portonovo, India. This dissertation was not available for review.

315. Jayabalan, N. and K. Ramamoorthi (1979). Significance of Ventral Luminescence of Silver-Bellies (Fam.:Leiognathidae). *Curr. Sci. (India)* 48(4):181-182.

The luminous system in leiognathids consists of a light organ containing symbiotic luminous bacteria, a reflector, a lens and accessory structures that direct, diffuse and transmit the light over the ventral surface of the body. This light appears to have multiple uses, including counterillumination and communication for aggregation and mating. A use in counterillumination may explain diel differences in depth distribution of leiognathids.

316. Jayabalan, N. and K. Ramamoorthi (1986). Luminescent System in the Ponyfish, *Leiognathus bindus* (Val). *Curr. Sci. (India)* 55(9):468-469.

The luminescent system of *Leiognathus bindus* consists of a light organ to harbor symbiotic luminous

bacteria, an airbladder reflector, translucent muscular lenses and accessory structures to produce, transmit and diffuse the luminescence of regulated intensity through its ventral surface, similar to other ponyfish. However, the male light organ is larger than that of the female and contains a ventral and lateral posterior dark region and lateral anterior opaque region which are absent in the female. It also contains lateral pigment granules that are absent in the female. These sexually dimorphic luminescence patterns suggest that the luminescence may function as a sexual recognition characteristic, as well as for ventral countershading.

317. Jensen, M. J., Bradley M. Tebo, Paul Baumann, M. Mandel and Kenneth H. Nealson (1980). Characterization of *Alteromonas hanedai* (sp. nov.), a Nonfermentative Luminous Species of Marine Origin. *Curr. Microbiol.* 3:311-315.

Eleven marine luminous isolates, which could not be identified with previously studied species of luminous marine bacteria, were subjected to an extensive characterization. The results indicated that these strains were phenotypically similar, had a G+C content in their DNA of 45 mol%, and differed from all previously characterized luminous species by their inability to ferment sugars. On the basis of these and other properties, the 11 luminous strains were assigned to the genus *Alteromonas* and given the species designation *A. hanedai*. Strain 281 (ATCC 33224) has been designated as the type strain of this new species.

318. Johnson, Carl H. and J. Woodland Hastings (1985). Bioluminescence and Chronobiology. In *Photobiology 1984*, J. W. Longworth, J. Jagger and W. Shropshire, eds., New York: Praeger Scientific, pp. 189-193.

Rhythms of bioluminescence in *Gonyaulax* are controlled by a biological clock modulating the intracellular concentration of both luciferin and luciferase. Luciferin is compartmentalized in subcellular granules distributed throughout the cell cortex. Bacterial luciferase genes have been cloned into *E. coli* and nucleotide encoding sequences for the alpha and beta subunits established. The primary emitter in the light-producing reaction has been identified.

319. Johnson, Carl H. and J. Woodland Hastings (1986). Biological Clock Control of Bioluminescence

in the Dinoflagellate *Gonyaulax*. *Plant Physiol.* 80(S4):92.

**ABSTRACT.** Circadian rhythms of bioluminescence in *Gonyaulax* are due not to fluctuations in the number of light-emitting organelles per cell but to oscillations in the cellular amount of both luciferin and luciferase.

320. Johnson, Carl H. and J. Woodland Hastings (1986). The Elusive Mechanism of the Circadian Clock. *Amer. Scientist* 74(1):29-36.

The dinoflagellate *Gonyaulax* exhibits four circadian rhythms which have been characterized: the capacity to fix carbon by photosynthesis; the timing of cell division; a spontaneous glow; and a capacity for flashing in response to stimulation. These rhythms are believed driven by a single pacemaker without feedback. External cues, such as the solar light cycle, monitor and entrain the pacemaker's phase and period, but are not part of the pacemaker. In the bioluminescence rhythms, the intracellular concentrations of both luciferin and luciferase and the activity of luciferase are rhythmically controlled. This fact suggests a general strategy of circadian control by regulation of short-lived rate-limiting enzymes.

321. Johnson, Carl H., J. Woodland Hastings and Shinya Inoue (1984). Bioluminescent Organelles in the Dinoflagellate *Gonyaulax*: Auto-Fluorescence and Circadian Rhythmicity. *Abstr., 3rd Int. Cong. Cell Biology*.

**ABSTRACT.** Bioluminescent flashes in *Gonyaulax polyedra* originate from discrete subcellular loci which colocalize with auto-fluorescent granules located in the cell cortex. This fluorescence is spectrally similar to bioluminescence and is lost subsequent to exhaustive stimulation of bioluminescence. The fluorescence and bioluminescence are restored in vitro by addition of purified luciferin, which fact suggests that it is due in vivo to luciferin. The intensity of fluorescence shows a circadian rhythm while the number of granules remains constant. Thus the cellular quantity of luciferin is regulated by the circadian clock.

322. Johnson, Carl H., J. Woodland Hastings and Shinya Inoue (1984). Circadian Auto-fluorescence of Bioluminescent Organelles in *Gonyaulax*. *Abstr., Soc. Cell Biology 24th Ann. Meet.*

**ABSTRACT.** Bioluminescent flashes in *Gonyaulax polyedra* originate from discrete subcellular loci which colocalize with auto-fluorescent granules located in the cell cortex. This fluorescence is spectrally similar to bioluminescence and is lost subsequent to exhaustive stimulation of bioluminescence. The fluorescence and bioluminescence are restored in vitro by addition of purified luciferin, which fact suggests that it is due in vivo to luciferin. The intensity of fluorescence shows a circadian rhythm while the number of granules remains constant. Thus the cellular quantity of luciferin is regulated by the circadian clock.

323. Johnson, Carl H., J. Woodland Hastings and Shinya Inoue (1984). Colocalization of Bioluminescence and Endogenous Fluorescence in Subcellular Sites of the Dinoflagellate *Gonyaulax polyedra*. *Biophys. J.* 45:220a.

**ABSTRACT.** Bioluminescence flashes in the dinoflagellate *Gonyaulax polyedra* originate from subcellular fluorescent granules which may be identical to "scintillons." The fluorescence appears to come from luciferin and disappears as bioluminescence decays, but with a lag.

324. Johnson, Carl H., J. Woodland Hastings and Shinya Inoue (1984). Image Intensified Recording of Colocalized Bioluminescent Flashes and Fluorescence from Subcellular Organelles in the Dinoflagellate *Gonyaulax*. *Society of General Physiologists, 38th Ann. Symp.*

**ABSTRACT.** An inverted microscope coupled to an image-intensified camera was used to observe that bioluminescent microflashes in *Gonyaulax* originate from discrete subcellular loci in the cell cortex that co-localize with auto-fluorescent granules. Fluorescence of the granules is spectrally similar to bioluminescence and disappears after exhaustive stimulation of bioluminescence, but is restored by the addition of purified luciferin. The fluorescence intensity exhibits a circadian rhythm.

325. Johnson, Carl H., J. Woodland Hastings and Shinya Inoue (1984). Circadian Rhythm of In Vivo Fluorescence of Subcellular Sites of Bioluminescence in the Dinoflagellate *Gonyaulax polyedra*. *Photochem. Photobiol.* 39(S):93S.

**ABSTRACT.** Bioluminescent flashes in the dinoflagellate *Gonyaulax polyedra* originate from

discrete subcellular loci that colocalize with autofluorescent granules. The fluorescence characteristics resemble and parallel those of bioluminescence, and fluorescence after stimulation of bioluminescence to exhaustion may be restored by adding luciferin. The fluorescence exhibits a circadian rhythm that parallels that of luciferin.

326. Johnson, Carl H., Shinya Inoue, Alan Flint and J. Woodland Hastings (1983). Compartmentalization of Algal Bioluminescence: Autofluorescence of Bioluminescent Particles in the Dinoflagellate *Gonyaulax* as Studied with Image-intensified Video Microscopy and Flow Cytometry. *J. Cell. Biol.* 100:1435-1446.

Compartmentalization of specialized functions to discrete locales is a fundamental theme of eucaryotic organization in cells. They report that bioluminescence of the dinoflagellate alga *Gonyaulax* originates in vivo from discrete subcellular loci that are intrinsically fluorescent. They demonstrate this localization by comparing the loci of fluorescence and bioluminescence as visualized by image-intensified video microscopy. These fluorescent particles appeared to be the same as the previously described in vitro "scintillons." They attribute the endogenous fluorescence to that of the bioluminescence substrate, luciferin, because (1) the fluorescence excitation and emission characteristics are comparable, (2) the autofluorescence is lost after exhaustive stimulation of bioluminescence and (3) the fluorescence of discharged particles in vitro can be restored by adding luciferin. The fluorescence in vivo exhibits a standard property of circadian (daily) rhythmicity: under constant environmental conditions, the intensity of the particle fluorescence fluctuates cyclically (it is maximal during the night phase and is low during the day). Thus, luciferin is localized within the cell at discrete loci from which the bioluminescence emanates; the cellular quantity of luciferin is rhythmically modulated by the circadian clock.

327. Johnson, Carl H., Marie-Thérèse Nicolas, J. Woodland Hastings and Shinya Inoue (1985). Immunogold Labelling of Bioluminescent Organelles in the Dinoflagellate Alga *Gonyaulax*. *Photochem. Photobiol.* 41(S):86S.

**ABSTRACT.** The autofluorescence of the granules that colocalize with the subcellular loci from which bioluminescent flashes in *Gonyaulax* originate

appears to be attributable to luciferin. Immunogold probes label two subcellular bodies, the trichocyst sheaths and "dense" vesicles. Electron and fluorescence microscopy shows that these vesicles and the autofluorescent granules appear to be the same.

328. Johnson, Carl H., James F. Roeber and J. Woodland Hastings (1983). Circadian Rhythm of Enzyme Amount Accounts for Rhythmic Activity Changes. *J. Cell Biol.* 97:397a.

**ABSTRACT.** ELISA immunoassays for luciferase and Western blots show that circadian variations in bioluminescence activity in *Gonyaulax* may be accounted for by changes in enzyme amounts.

329. Johnson, Carl H., James F. Roeber and J. Woodland Hastings (1984). Circadian Changes in Enzyme Concentration Account for Rhythm of Enzyme Activity in *Gonyaulax*. *Science* 223:1428-1430.

A circadian rhythm in the activity of luciferase is partly responsible for rhythmic bioluminescence in the dinoflagellate alga *Gonyaulax polyedra*. The cyclic activity of this enzyme can be attributed to a corresponding rhythm in the concentration of immunologically reactive luciferase protein. Hence protein turnover (synthesis or degradation or both) is used by the endogenous clock to control the daily rhythm of bioluminescence.

330. Johnson, Frank H. and Osamu Shimomura (1982). Newer Outlooks on Bioluminescence, Including Recent Research on Euphausiid Shrimps. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk. Akad. Nauk USSR, pp. 69-88.

A concise, elegant history of bioluminescence research from Dubois to the present is provided. Classic systems (*Pholas*, *Cypridina*, fireflies, euphausiids, coelenterates) are described. Organisms exhibiting luciferin-luciferase and photoprotein systems are tabulated.

331. Johnston, I. A. and Peter J. Herring (1985). The Transformation of Muscle into Bioluminescent Tissue in the Fish *Benthalbella infans* Zugmayer. *Proc., R. Soc. London* B225:213-218.

The luminescent tissue of the pelvic and anal organs of the scopolarchid fish *Benthalbella infans* Zugmayer is derived from skeletal muscle. Normal

muscle cells are found to be interspersed between fibers containing "granules" 0.5-2µm in diameter. The majority of granules are bounded by a double membrane and filled with an electron-dense material which is presumably a component of the luminescent system. All fibers with granules contain remnants of myofibrils, although there is a wide variation in their ultrastructure. In some cases, relatively few granules are present and the myofilament lattice structure and the sarcotubular system of myofibrils appear normal. Other fibers are almost entirely filled with granules and only isolated fragments of degenerating myofibrils and free filaments are present. In these fibers, there are relatively few mitochondria and glycogen granules are more numerous than in normal muscle fibers. Some of the dense granules are not bounded by a distinct membrane; they have a diffuse periphery and "empty" luminescent vesicles containing small amounts of electron-dense material are always present. Lysosomes are common to all muscle fibers containing granules and frequently enclose complete granules, suggesting their involvement in the turnover or processing of luminescent material. The modification of muscle fibers for other physiological purposes, and the origin of luminous tissue in scopolarchid fish are briefly discussed.

332. Kaplan, Heidi B. and E. P. Greenberg (1985). Diffusion of Autoinducer is Involved in Regulation of the *Vibrio fischeri* Luminescence System. *J. Bacteriol.* 163(3):1210-1214.

The enzymes for luminescence in *Vibrio fischeri* are induced by the accumulation of a species-specific metabolite (autoinducer) in the culture medium. Tritium-labeled autoinducer was used to study the mechanism of autoinduction. When <sup>3</sup>H-autoinducer was added to suspensions of *V. fischeri* or *E. coli*, cellular concentrations equaled external concentrations. For *V. fischeri*, equilibration of <sup>3</sup>H-autoinducer was rapid (within 20 sec) and >90% of the cellular tritium remained in unmodified autoinducer. When *V. fischeri* or *E. coli* cells containing <sup>3</sup>H-autoinducer were transferred to autoinducer-free buffer, 85 to 99.5% of the radiotracer escaped from the cells, depending on the strain. Concentrations of autoinducer as low as 10 nM, which is equivalent to 1 or 2 molecules per cell, were sufficient for induction and the maximal response to autoinducer occurred at about 200 nM. If external autoinducer concentrations were decreased to below 10 nM after induction had commenced, the

induction response did not continue. Based on this study, a model for autoinduction is described wherein autoinducer association with cells is by simple diffusion and binding of autoinducer to its active site is reversible.

333. Kaplan, Heidi B., E. P. Greenberg, Anatol Eberhard and Cidra A. Widrig (1984). Autoinduction of Luminescence in *Vibrio fischeri*: Use of Radiolabeled Inducer in Mechanistic Studies. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 84:137.

**ABSTRACT.** Tritium-labeled autoinducer was used to study the association of autoinducer with cells of an autoinducer-deficient strain of *Vibrio fischeri*. Experimental evidence supported a model of induction whereby autoinducer associates with *V. fischeri* cells by diffusion and a certain amount of the associated autoinducer is bound to the cells.

334. Karl, David M. and Kenneth H. Nealson (1980). Regulation of Cellular Metabolism During Synthesis and Expression of the Luminous System in *Beneckea* and *Photobacterium*. *J. Gen. Microbiol.* 117:357-368.

Parameters of cellular energetics (ATP pools, adenylate energy charge, GTP pools and oxygen consumption), as well as bioluminescence and growth, have been examined in batch cultures of four different species of luminous bacteria. The findings indicate that all of these energetic parameters remain constant throughout the growth cycle while bioluminescence is induced and increases many fold. These observations hold true for very bright strains during their dim and bright phases of growth, as well as for a luminescence-conditional strain under bright or dark conditions. The percentage of the total oxygen consumption that was due to bioluminescence was shown to vary by as much as a factor of  $10^3$  during growth. For very bright cells, the oxygen consumption experiments suggest both that the energetic requirements of the bioluminescent system are significant and that the quantum efficiency  $Q_{O_2}$  of the luciferase in vivo is quite high, possibly approaching 1.0. Similar considerations based on ATP pool size and energetic estimates of luminescence indicate that the luminous system in bright cells represents a small but possibly significant energy drain. Finally, two methodological features are discussed. First, it was shown that extracts of cells that have been grown in media devoid of inorganic phosphate contain a

heat-stable ATPase activity, which can lead to falsely low ATP values. Second, it was shown that the interfering effect of GTP on the assay of ATP could be completely overcome by the addition of GDP to the assay mixture.

335. Kelly, Mahlon G. and Paul Tett (1978). Bioluminescence in the Ocean. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 399-417.

This article discusses the general ecological role of marine luminescence, the extent to which dinoflagellates are responsible for background bioluminescence and the environmental factors determining the occurrence of both normal luminescence and luminous displays. It is primarily a shortened version of an earlier article by the same authors (P. B. Tett and M. G. Kelly, 1973, "Marine Bioluminescence," *Oceanogr. Mar. Biol. Ann. Rev.* 11:89-173).

336. van Keuren, Jeffrey, Howard Gordon and Elijah Swift (1986). Remote Sensing of Bioluminescence from Diverse Oceanic Regions. *Biowatt News* 6:6 (September).

**ABSTRACT.** The distribution of bioluminescence signal strength and duration depends on the bioluminescent community in selected oceanic regions and can be used to characterize the community. The vertical distributions of the signal are known and propagation depends on the distribution of optical variability, the major source of which is the distribution of chlorophyll-containing phytoplankton. Thus the strength of the bioluminescence signal at the sea surface available for remote sensing varies from region to region, depending on the biological community, and on its origination depth and the optical attenuation due to phytoplankton.

337. van Keuren, Jeffery, Elijah Swift, Harold P. Batchelder and William H. Biggley (1987). Twilight and Moonlight Measurements in the Northwest Atlantic During May and August 1987. *EOS* 68(50):1745.

**ABSTRACT.** A sensor has been developed to define the light regime at dusk and dawn. It is sufficiently sensitive to record changes in moonlight induced by partial cloud cover. Ambient light is related to changes in bioluminescence potential in the

water column (through vertical migration of luminous species and photoinhibition) and vertical movements of acoustic scattering layers of zooplankton.

338. Kiessig, Richard S., Jeffrey M. Hertz and Beatrice M. Sweeney (1979). Shifting the Phase of the Circadian Rhythm in Bioluminescence in *Gonyaulax* with Vanillic Acid. *Plant Physiol.* 63(2):324-327.

Exposure for 4 hours to vanillic acid (4-hydroxy 3-methoxy benzoic acid) caused large delay phase shifts (5 to 6 hours) in the circadian rhythm of bioluminescence in *Gonyaulax polyedra*, when assayed at either 10 to 14 circadian time or 22 to 02 circadian time in constant light and temperature, provided that the pH of the medium was 7.1 or lower. Corresponding changes in the pH with acetic acid did not shift phase. Vanillic acid caused detectable depolarization of the membranes of *Gonyaulax*, as demonstrated with the cyanine dye fluorescence technique.

339. Kils, U. (1979). Performance of Antarctic Krill *Euphausia superba*, at Different Levels of Oxygen Saturation. *Meeresforsch.* 27:35-47.

The effects of low oxygen saturations on survival, swimming performance and luminescence of krill have been investigated and the lethal  $O_2$  saturation and the critical  $O_2$  saturation were determined. A high sensitivity to low oxygen tensions, but an ability for adaptation became evident. At  $O_2$  saturations lower than 90% the animals no longer luminesced. The correlation on vertical krill distribution and oxygen regime is discussed. Respiration rates in the light and dark and at different  $O_2$  tensions have been determined.

340. Kito, Y., M. Seidou, M. Michinomae and A. Tokuyama (1987). Photic Environment, Bioluminescence and Vision of a Squid, *Watasenia scintillans*. *Zool. Sci. (Tokyo)* 4(6):1107.

**ABSTRACT.** The half bandwidth of light from the large photophores of the fourth arm of *Watasenia scintillans* is broad with a maximum at 475 nm. Both the bandwidth and emission maximum of light from the large photophores of the arm and the small photophores of the mantle vary according to the characteristic shapes and colors of the photophores. Two fluorescent substances, with emission maxima of 460 and 490 nm, can be isolated from the small mantle photophores. Thus, the variations in the

spectral characteristics of light emission can be explained as due to mixtures of these two substances in varying relative concentrations. The emission characteristics correlate with the wavelength sensitivity of a trichromatic visual pigment found in the eyes of the squid rather than with the wavelength of maximum transmissivity of sea water.

341. Kluge, Manfred (1982). Biochemical Rhythms in Plants. In *Biological Timekeeping*, J. Brady, ed., Cambridge (U.K.): Cambridge University Press, pp. 159-172. (*Soc. Exp. Biol. Seminar Series* 14:159-172).

A general introduction to biochemically determined rhythmic phenomena in plants is provided. The circadian rhythms of *Gonyaulax* are discussed and several explanatory theories are put forth along with supporting evidence.

342. Korgen, Ben J. (1986). Lighted Houses in the Sea. *Sea Frontiers* 32(1):4-10.

Bioluminescence in larvaceans is described. Bioluminescence occurs not only in the trunk of the larvacean, but also in the transparent, gelatinous house that it secretes around itself using mucous and frequently discards. Abandoned houses can flash upon stimulation for up to 4 hours after separation.

343. Kornicker, Louis S. (1987). Supplementary Description of *Cypridina americana* (Muller, 1890), a Luminescent Myodocopid Ostracode from the East Pacific. *Proc., Biol. Soc. Wash.* 100(1):173-181.

The original description by Muller in 1890 of *Cypridina americana*, the only representative of the genus known from the vicinity of the Americas and one of the two luminescent myodocopid ostracode species known from the East Pacific, consists of two short paragraphs and a single illustration of the carapace and is inadequate for recognition of the species. The supplementary description is in considerable detail and all appendages are illustrated.

344. Koslow, J. Anthony (1979). Vertical Migrators See the Light? *Limnol. Oceanogr.* 24(4):783-784.

"Spontaneous" bioluminescent flashing at night may be due to active zooplankton disturbing the emitting organisms. This light may make the zooplankters vulnerable to visually orienting predators and may explain the adaptive significance of dinoflagellate bioluminescence. This hypothesis is

supported by a decline in copepod feeding in the presence of luminous dinoflagellates and by the escape response of some luminous migratory copepods, which excrete a luminous cloud while darting away when attacked. Further support for this theory would be provided if vertically migrating zooplankters entered the upper waters and grazed most intensely in late afternoon. This behavior is seen in migration of the copepod *Calanus*.

345. Kosower, E. M. (1980). A Proposed Mechanism for Light Emission by Bacterial Luciferase Involving Dissociative Electron Transfer. *Biochem. Biophys. Res. Comm.* 92(2):356-364.

A new mechanism that involves dissociative electron transfer in the energy transducing step is set forward for bacterial luciferase catalyzed light emission. The proposal involves (1) dissociation of the 4a-hydroperoxyflavin to a flavin radical and .02, accounting for 570 and 620 nm absorption; (2) .02-addition to the aldehyde carbonyl to form a peroxy radical; (3) abstraction of H from an enzyme thiol group to form RCH(OOH)OH; (4) thiyl radical abstraction of the H on C in RCH(OOH)OH, a step which can show a  $k_p/k_d$  of ca. 4; and (5) dissociative electron-transfer, a highly exothermic step that leads to a protonated flavin excited state, a carboxylic acid and water.

346. Krasnow, Richard, Jay C. Dunlap, Walter Taylor, J. Woodland Hastings, William Vetterling and Van D. Gooch (1980). Circadian Spontaneous Bioluminescent Glow and Flashing of *Gonyaulax polyedra*. *J. Comp. Physiol.* B138:19-26.

A new, fully computerized method for the measurement and analysis of dinoflagellate bioluminescence has been developed and applied to the spontaneous light emission of *Gonyaulax polyedra*. This light emission consists of a low-level steady glow and occasional superimposed flashes. The instrumentation distinguishes the two components and records them separately; both exhibit circadian rhythmicity. In this paper they describe the method in detail and show results for flashing and glow measured under light-dark cycles and under constant light of different intensities. Under constant dim light at 19°C, both rhythms exhibit two peaks during a circadian cycle; the minor ones occur approximately 9 hours before the major ones. Under these conditions the major flashing peak occurs early during the

subjective night and the major glow peak at the end, about 9 hours later. However, the relative phase angle between glow and flashing peaks varies with light intensity, being as little as 220 min (3.7 h) in the dark under light-dark entrained conditions, to as much as 700 min (11.7 h) in dim light under free-running conditions. The ambient light intensity also affects differentially the amount of light emitted in the two modes of spontaneous luminescence. These results suggest that the controls for the two processes must at some point diverge.

347. Krasnow, Richard, Jay Dunlap, Walter Taylor, J. Woodland Hastings, William Vetterling and Elisha Haas (1981). Measurements of *Gonyaulax* Bioluminescence, Including That of Single Cells. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis (Minnesota): Burgess Publishing Co., pp. 52-63.

The dinoflagellate *Gonyaulax* emits light in three forms: a spontaneous low level glow; rapid spontaneous flashes lasting about 100 msec; and stimulated flashing by various means of stimulation. All three exhibit circadian rhythms. These rhythms are characterized and flash and glow intensities and kinetics are measured. A model for a relationship among the three types of emission is suggested. Individual cells are found to behave quite differently from the average of a population.

348. Krasnow, Richard, Walter R. Taylor, Jay C. Dunlap and J. Woodland Hastings (1979). Computerized Measurements of Circadian Bioluminescence in *Gonyaulax*. *Abstr., Amer. Soc. Photobiol.* 7th Ann. Meet., p. 69.

**ABSTRACT.** Computerized instrumentation for studying circadian rhythm of bioluminescence in *Gonyaulax* is described. The total amount of light emitted per cell per day, both spontaneously and stimulated mechanically or by acid, is about  $10^8$  quanta. Spontaneous flashing peaks about five hours before the glow, but this phase relation appears to depend on the environment.

349. Krasnow, Richard, William Vetterling, Elisha Haas, Jay C. Dunlap, Walter Taylor and J. Woodland Hastings (1982). Computer Analysis of Light Emission and Circadian Rhythms of Luminescence in Populations and in Single Cells of the Dinoflagellate *G. polyedra*. In *Bioluminescence in the Pacific*,

I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 150-164.

Separate but possibly linked circadian rhythms are reported for spontaneous flashing and glowing in *G. polyedra*. The flashing activity peak coincides with the maximum for stimulated luminescence and precedes the glow peak by several hours. The average number of spontaneous flashes per cell is 0.9/cell-day. The average intensity of the glow is  $0.9 \times 10^8$  quanta/cell, or about 1 quantum/cell-msec. The flashes exhibit a variety of kinetics, but the majority exhibit a full width at half height of 27 msec. Higher light intensities during photophase inhibit spontaneous flashing but not glow. Attempts to stimulate flashing using a sinusoidally driven piezoelectric cylinder to create a pressure wave just below cavitation amplitude show no effect. Single cell measurements show considerable deviations from average, with many lacking either the glow or spontaneous flashing rhythm. Cell collisions and light flashes do not appear to cause spontaneous flashing; flashing and glow capacities appear to be independent.

350. Kratasyuk, G. A. and V. N. Petushkov (1984). Biochemistry of Bacterial Bioluminescence. In *Luminescent Bacteria* (English translation of *Svetyashchiyessya Bakterii*, Ye. N. Kondrat'yeva, ed., Moscow: Izdatel'stvo "Nauka"), pp. 156-189, JPRS-UBB-85-018-L, 31 October 1985.

Chemiluminescence and bioluminescence are defined and various reaction mechanisms are briefly presented, along with the structures of six luciferins. The mechanism of bacterial bioluminescence is then presented in detail, and the cofactors involved are identified and discussed with regard to their roles. Differences in bacterial luciferases are discussed and a number of constants and spectra are given. Various hypotheses concerning the emitting species and the nature of bacterial luciferase are presented and discussed in detail. The quantum yields are determined for various reactions. The molecular weights of luciferase subunits from different species are compared.

351. Kuzmanov, Zoran (1983). Bioluminescent Phenomena Observed in the South China Sea. *Mar. Obs.* 53:85-91.

A highly detailed and lyrically descriptive depiction of a complex phosphorescent wheel pattern is given.

352. Labas, Yu. A. (1982). Triggering Mechanisms and Adaptive Significance of the Bioluminescence in Ctenophores. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 136-149.

The kinetics of the light response of *Bolnopsis* to stimulation resembles that of the skeletal muscle-toothed tetanus. Changes in the flash amplitude and shape are not accompanied by changes in the peak depolarizing potential. These observations suggest that bioluminescence in this genus is used to repel or disorient predators or to alert others to the presence of a predator.

353. Labas, Yu. A. (1984). Behavioral Functions of Bioluminescence. In *Proc., Third All-Union Conf. on Animal Behavior*, Vol. 2, *Behavior of Animals in Communities*, A. A. Zakharov, ed., Moscow: Izdatel'stvo Nauka, pp. 45-46.

This paper was not available for review.

354. Lapota, David (1983). Bioluminescence in the Marine Ostracod *Cypridina americana* (Müller, 1890) off Manzanillo, Mexico (Myodocopa: Cypridininae). *Proc., Biol. Soc. Wash.* 96(2):307-308.

A myodocopid ostracod, *Cypridina americana* (Müller, 1890), found in coastal waters off Manzanillo, Mexico, was observed to be bioluminescent. Collection of this ostracod extends the known geographic distribution of this little-studied species and documents the only observation of bioluminescence in a species of *Cypridina* found in Eastern Pacific coastal waters.

355. Lapota, David (1987). Planktonic Bioluminescence Measurements in Arctic Waters. *EOS* 68(50):1695.

**ABSTRACT.** Bathyphotometer measurements of bioluminescence at high latitudes, even under pack ice, have recorded intensities in summer comparable to open and coastal water bioluminescence intensities recorded elsewhere. Measurements have been performed in Vestfjord, Norway, and in the Beaufort Sea near Point Barrow, Alaska. In Vestfjord maximum bioluminescence of  $3 \times 10^8$ – $2 \times 10^9$  photons/sec/ml was found 15–30 m below the surface. The intensity at 90–100 m ranged from  $3 \times 10^6$ – $4 \times 10^7$  photons/sec/ml. In the Beaufort Sea layering was found in the upper 50 m, with intensities of  $3 \times 10^6$ – $2 \times 10^8$  photons/sec/ml.

Major causative organisms were the copepod *Metridia longa* and *Protoperidinium* dinoflagellates.

356. Lapota, David and Jon R. Losee (1982). Observations of Bioluminescence in Marine Plankton from the Gulf of California. *EOS* 63(45):944.

**ABSTRACT.** Using a newly designed laboratory plankton test chamber, bioluminescence was observed on a cruise in the Gulf of California in dinoflagellates, copepods and larval euphausiids. The chamber can be used to test large numbers of organisms individually to confirm pumped system measurements of bioluminescence and to confirm or refute bioluminescence in the tested organism.

357. Lapota, David and Jon R. Losee (1983). Records of Bioluminescence in Marine Plankton from the Norwegian Sea and Waters off North Cape. *EOS* 64(52):1102.

**ABSTRACT.** Flash characteristics were recorded on the Varifront V research cruise in the Norwegian and Barents Seas in May, 1983 from 175 isolates representing dinoflagellates of the genera *Protoperidinium* and *Ceratium*, copepods of the genus *Metridia*, ostracods of the genus *Conchoecia*, euphausiid shrimp, tomopterid worms, beroid ctenophores, colonial radiolarians and siphonophores. Average light output per flash ranged from  $2 \times 10^8$  photons (colonial radiolarians) and  $6.2 \times 10^8$ – $1.8 \times 10^9$  photons (*Ceratium* and *Protoperidinium*, respectively) to  $4.6 \times 10^{11}$  photons (*Metridia longa*). All other organisms tested, including *Metridia lucens*, exhibited intermediate light emission values.

358. Lapota, David and Jon R. Losee (1984). Observations of Bioluminescence in Marine Plankton from the Sea of Cortez. *J. Exp. Mar. Biol. Ecol.* 77:209–240.

A bioluminescence chemical oceanography research cruise (*Varifront III*) through the Sea of Cortez from November through December 1981 provided an opportunity to investigate plankton associated with a brilliant and extensive display of surface water bioluminescence at the north end of Balle-as Channel. New observations of bioluminescence were made on larval stages of the euphausiid *Nyctiphanes simplex* Hansen (Calyptopis II, Furcilia I, II and III and juveniles) and *Euphausia eximia* Hansen (Calyptopis I), the Calanoida copepods *Centropages furcatus* Dana, *Paracalanus indicus*

Wolfenden, *Acrocalanus longicornis* Giesbrecht, the Cyclopoida copepods *Corycaeus* (*Corycaeus*) *speciosus* Dana, *Corycaeus* (*Onychocorycaeus*) *latus* Dana and several dinoflagellates *Ceratium breve* Ostensfeld and Schmidt, *Ceratium horridum* Gran and *Ceratium gibberum* Gouret. These observations indicate the increasing importance of some of the smaller copepods and larval euphausiids contributing to surface bioluminescence.

359. Lapota, David, Jon R. Losee and Mark L. Geiger (1986). Bioluminescence Displays Induced by Pulsed Light. *Limnol. Oceanog.* 31(4):887–889.

Unusual displays of bioluminescence apparently stimulated by pulsed light from a handheld flashlight were observed from the surface in an ice pond in the Beaufort Sea and from a submersible at a depth of 600 m, 64 km off the east coast of Florida.

360. Lapota, David, Jon R. Losee, H. Douglas Huddell, Charles P. Galt, Kenneth H. Nealson and James K. Orzech (1985). Measurements and Observations of Bioluminescence in the Western Indian Ocean and Arabian Sea. *EOS* 66(51):1320–1321.

**ABSTRACT.** Bioluminescence was measured in the western Indian Ocean and Arabian Sea during the Southwest Monsoon (July) in 1985. Bioluminescence was measured from two species of *Pyrocystis*, several species of *Protoperidinium*, *Noctiluca miliaris* and *Ceratocorys horrida*, all dinoflagellates. The principle contributors to surface bioluminescence appeared to be *Pyrocystis* dinoflagellates, *Pleuromamma* copepods, larval euphausiids, ostracods and radiolarians. A "milky" sea was observed and a luminous bacterium apparently associated with mucoid aggregates was isolated from its waters.

361. LaRivière, Luc and Michel Anctil (1984). Uptake and Release of [<sup>3</sup>H]-Serotonin in Photophores of the Midshipman Fish, *Porichthys notatus*. *Comp. Biochem. Physiol.* 78C(1):231–239.

A kinetic analysis of [<sup>3</sup>H]-5-HT uptake in the photocytes of the photophores of *Porichthys notatus* revealed a high affinity ( $k_m: 1.71 \times 10^{-7}$ ) and low affinity component ( $k_m: 1.10 \times 10^{-5}$  M). The high affinity uptake was sodium- and potassium-dependent but largely insensitive to temperatures between 0° and 20°C. Ouabain ( $5 \times 10^{-3}$  M) and dinitrophenol ( $10^{-3}$  M) reduced uptake significantly. DMI, imipramine and

fluoxetine, in that order of potency, greatly inhibited [ $^3\text{H}$ ]-5-HT uptake. Noradrenaline and adrenaline reduced uptake in a noncompetitive manner, while dopamine, tryptophan, 5-hydroxytryptophan and *Cypridina* luciferin had little or no effect on uptake. Nonfacilitated luminescent responses to electrical stimulation were accompanied by release of [ $^3\text{H}$ ]-5-HT accumulated in the photocytes. Facilitatory luminescence excitation consistently failed to induce the release of [ $^3\text{H}$ ]-5-HT. Electrical and adrenaline ( $10^{-5}\text{M}$ ) stimulation of photophores after [ $^3\text{H}$ ]-5-HT release has occurred, failed to elicit any additional luminescent response. The photophores were responsive to KCN ( $10^{-3}\text{M}$ ) under these conditions. The results indicate that a specific carrier-mediated transport system is responsible for photocytic [ $^3\text{H}$ ]-5-HT uptake and that release of photocytic [ $^3\text{H}$ ]-5-HT is stringently regulated and followed by inhibition of luminescence excitability.

362. Latz, Michael I. (1983). Control of Bioluminescence in the Midwater Shrimp, *Sergestes similis*. Ph.D. Dissertation, University of California, Santa Barbara.

The midwater shrimp, *Sergestes similis* Hansen, possesses five organs of Pesta, hepatic light organs that constitute about 20% of the opaque body structures. The posterior light organ and eyestalk counterrotate during transverse body tilt to compensate for body inclination and preserve the effectiveness of counterillumination. This rotation is statocyst mediated and is not affected by directional illumination. *Sergestes similis* is initially unresponsive to dim light and does not reach maximal bioluminescent counterilluminating response for about 25 min after the onset of stimulation. This priming process perhaps involves hormonal control.

363. Latz, Michael I. (1985). Does Bioluminescence in the Colonial Radiolaria Originate from Algal Symbionts? *Amer. Zool.* 25(4):27a.

**ABSTRACT.** A comparison of the luminescence of mechanically stimulated radiolarians to that of free-living dinoflagellates suggests that luminescence of the radiolaria does not originate from symbiotic luminous dinoflagellates.

364. Latz, Michael I. and James F. Case (1980). Structure and Function of the Photophores of the

Midwater Shrimp, *Sergestes similis*. *Amer. Zool.* 20(4):851.

**ABSTRACT.** Light emission in *Sergestes similis* is confined to discrete areas of the ventral surface of the organs of Pesta. Only the luminescent tissue is fluorescent. The photophores are ventrally oriented tubules capped dorsally with screening pigment. They are maintained in a downward orientation, regardless of the body tilt of the shrimp, by rotation within the body.

365. Latz, Michael I. and James F. Case (1982). Light Organ and Eyestalk Compensation to Body Tilt in the Luminescent Midwater Shrimp, *Sergestes similis*. *J. Exp. Biol.* 98:83-104.

The posterior light organ and eyestalk of the midwater shrimp, *Sergestes similis* Hansen, are capable of  $140^\circ$  of angular movement within the body during pitch body tilt, maintaining the organs at near horizontal orientations. Counter rotations compensate for 74-80% of body inclination. These responses are statocyst mediated. Unilateral statolith ablation reduces compensation by 50%. There is no evidence for either homolateral or contralateral control by the single functioning statocyst. Bilateral lith ablation abolishes counter rotation. Light organ and eyestalk orientations are unaffected by the direction of imposed body tilt. Bioluminescence is emitted downward from horizontal animals with an angular distribution similar to the distribution of oceanic light. The amount of downward directed luminescence in tilted animals decreases at large angles of body inclination due to less than total compensation by the light organs. Eye turning towards a light source is induced by upward-directed illumination. The resulting change in eyestalk orientations never amounts to more than  $25^\circ$ . The turning is abolished by bilateral statolith ablation. Downward-directed illumination, comparable in intensity to oceanic light, generally does not generate significant eye turning. Light organ orientations remain unaffected by directional illumination, both before and after bilateral statolith ablation. The compensatory counter rotations by the posterior light organ and eyestalk suggest that counter illumination by *S. similis* remains effective in inclined animals.

366. Latz, Michael I. and James F. Case (1983). Priming of Bioluminescent Countershading in a Midwater Shrimp. *Amer. Zool.* 23(4):940.

**ABSTRACT.** The midwater shrimp, *Sergestes similis*, initially does not exhibit a countershading response to stimulation by dim light. Several minutes after the onset of stimulation, a response begins, which reaches maximum intensity after about 25 min. Upon return to the dark, the fast countershading response reverts back to the slow response of unstimulated animals.

367. Latz, Michael I., James F. Case and Tom D. Dickey (1986). Bioluminescence Stimulated by Fluid Shear Related to Water Column Shearing in the Sargasso Sea. *Biowatt News* 6:9 (September).

**ABSTRACT.** Bioluminescence is stimulated in samples collected by net tows in the Sargasso Sea by shear generated by two methods: (1) couette flow generated by an outer cylinder rotating around a concentric inner cylinder; and (2) a disk rotating in a large chamber. Shear stress alone is sufficient to induce light emission. Bioluminescence is stimulated by couette flow at the lowest available shear stress of 2 dynes  $\text{cm}^{-2}$  and reached a maximum at about 7 dynes  $\text{cm}^{-2}$ . The majority of the emission is probably due to the dinoflagellate *Pyrocystis* and the response pattern is similar to that observed for *Gonyaulax* in the laboratory. In situ ocean shearing due to mixing is measured at two orders of magnitude less than the level known to stimulate bioluminescence and is probably insufficient to generate light emission.

368. Latz, Michael I., James F. Case and Robert L. Gran (1986). Excitation of Bioluminescence by Fluid Shear. *EOS* 67(44):970.

**ABSTRACT.** Smoothly increasing steady shear fields were established by (1) Couette flow established between a stationary inner cylinder and a rotating outer cylinder and (2) boundary layer flow on a spinning disk (von Karman flow). In both cases, shear stresses less than about 1 dyne/ $\text{cm}^2$  did not excite light emission above the spontaneous level. At higher shear stresses light output was proportional to the third power of the local stress up to 35 dynes/ $\text{cm}^2$  for cultured dinoflagellates and 6 dynes/ $\text{cm}^2$  for collected mixed plankton. Prolonged constant level stimulation resulted in an exponential decrease in light output with time. This is consistent with a constant fractional rate of depletion of the stimutable population.

369. Latz, Michael I., Tamara M. Frank, Mark R. Bowlby, Edith A. Widder and James F. Case (1987).

Variability in Flash Characteristics of a Bioluminescent Copepod. *Biol. Bull.* 173(3):489-503.

Bioluminescence of the copepod, *Pleuromamma xiphius*, was investigated with an optical multichannel analyzer (OMA) to measure emission spectra, an integrating sphere-photon counting detector system to determine flash kinetics and quantum emission and an ISIT video system to image spatial patterns of emission. Light emission was in the blue spectral region, with maximum emission at approximately 492 nm. Spectral waveforms were unimodal, or bimodal with the secondary peak at 472 nm. Flashes in response to a single stimulus consisted of two components: a fast component attaining maximum intensity in under 100 msec and a slow element which peaked after 600 msec. The fast component originated from thoracic and abdominal light organs while the slow component represented a large expulsion of luminescent material from the abdominal organ only. Both components exhibited first-order exponential decay although the decay rate of the fast component was approximately one order of magnitude greater. The typical flash response to a single stimulus exhibited a response latency of 30 msec, initial rise time of 87 msec, duration of 2.4 sec and quantum emission of  $1.4 \times 10^{10}$  photons flash $^{-1}$ . Quantum emission increased with increasing stimulus strength. Both response waveform and total quantum emission were affected by the frequency of electrical stimuli. Stimulation at 1 Hz generated the greatest luminescence, averaging  $1.1 \times 10^{11}$  photons response $^{-1}$  for 11 sec emissions. Higher rates of stimulation decreased total quantum emission and response episode duration and resulted in greater temporal summation of the emission waveform. Variability in flash characteristics due to electrical stimulation suggests a versatility of luminescent displays in situ.

370. Latz, Michael I., Tamara M. Frank and James F. Case (1985). Zooplankton Bioluminescence in the Sargasso Sea: Spectral and Temporal Characteristics. *EOS* 66(51):1313.

**ABSTRACT.** Bioluminescence spectra and kinetics have been measured from 40 species of organisms found in the upper 100 m of the waters in the Sargasso Sea using an optical multichannel analyzer and compared to the spectral composition of oceanic irradiance. Emission maxima were between 445 and 490 nm, bracketing the peak transmission of downwelling irradiance. Most emission was in the

form of flashes. In the copepod *Pleuromamma* and radiolarians these flashes exhibited rise times of 100–400 msec and durations of 1–10 sec.

371. Latz, Michael I., Tamara M. Frank and James F. Case (1985). Characterization of Bioluminescence in Plankton of the Sargasso Sea during BIOWATT I. In *Data Directory for BIOWATT I, R/V Knorr, 1-26 April 1985*, pp. 15-18.

A preliminary account of research performed during the BIOWATT I cruise is given. An attempt to measure the threshold shear stress for stimulation of bioluminescence in dinoflagellates and copepods is reported. Studies of emission spectra of 40 taxa from 7 phyla, most never previously measured, are reported. The characterization of single flashes of colonial radiolaria and the copepod *Pleuromamma* by response kinetics and energy content is performed.

372. Latz, Michael I., Tamara Frank and James F. Case (1986). Spectral Composition of Bioluminescence of the Sargasso Sea. *Biowatt News* 3:4 (April).

**ABSTRACT.** Bioluminescence spectra from approximately 50 species in 7 phyla from the upper 100 m of the water column were measured during the April, 1985, Biowatt cruise in the Sargasso Sea. Most emission occurred between 440 and 490 nm, close to the maximum transmission window of 450–470 nm. An exception was the polychaete worm *Tomopteris*, which emitted at 565 nm. Light emission from individual photophores of the squid, *Leachia lemur*, generated similar waveforms but shifted emission maxima. However, individual copepods of the species *Pleuromamma xiphioides* showed similar emission maxima but differences in the fine structure of the waveforms. The shrimp *Systellaspis debilis* exhibited two modes of light emission: (1) luminescent spew; and (2) emission from cuticular photophores, each displaying a different spectrum.

373. Latz, Michael I., Tamara M. Frank, James F. Case, Elijah Swift and Robert R. Bidigare (1987). Bioluminescence of Colonial Radiolaria in the Western Sargasso Sea. *J. Exp. Mar. Biol. Ecol.* 109:25–38.

Colonial radiolaria (Protozoa: Spumellarida) were a conspicuous feature in surface waters of the Sargasso Sea during the April 1985 Biowatt cruise. The abundance of colonies at the sea surface at one

station was estimated to be 23 colonies  $m^{-2}$ . Bioluminescence by colonial radiolaria, representing at least six taxa, was readily evoked by mechanical stimuli and measured by fast spectroscopy and photon-counting techniques. Light emission was deep blue in color (peak emissions between 443 and 456 nm) and spectral distributions were broad (average half bandwidth of 80 nm). Single flashes were 1–2 sec in duration at about 23°C, with species-dependent kinetics which were not attributed to differences in colony morphology, since colonies similar in appearance could belong to different species (even families) and display different flash kinetics. Although the presence of dinoflagellate symbionts was confirmed by the presence of dinoflagellate marker pigments in the colonies, luminescence in the radiolaria examined most likely did not originate from symbiotic dinoflagellates because of (1) differences in the emission spectra, (2) unresponsiveness to low pH stimulation, (3) differences in flash kinetics and photon emission of light emission and (4) lack of light inhibition. The quantal content of single flashes averaged  $1 \times 10^9$  photons flash<sup>-1</sup> and colonies were capable of prolonged light emission. The mean value of bioluminescence potential based on measurements of total mechanically stimulated bioluminescence was  $1.2 \times 10^{11}$  photons colony<sup>-1</sup>. It is estimated that colonial radiolaria are capable of producing about  $2.8 \times 10^{12}$  photons  $m^{-2}$  of sea surface. However, this represented only 0.5% of in situ measured bioluminescence potential.

374. Lavi, Jukka, Raimo Raunio, Yuri A. Malkov and Timo Lövgren (1983). The Effect of Luciferase and NADH:FMN Oxidoreductase Concentrations on the Light Kinetics of Bacterial Bioluminescence. *Biochem. Biophys. Res. Comm.* 111(1):266–273.

The effects of NADH:FMN oxidoreductase and luciferase concentrations on the light kinetics of the bacterial bioluminescent reaction were investigated. Light emission with low decay rates was obtained by regulating the conversion of NADH to NAD<sup>+</sup> by controlling oxidoreductase activity. Constant light emission can be obtained when the oxidoreductase activity is below 2.5 U/l in the assay system. The luciferase concentration affects the light intensity but it has no effect on the decay rate of light emission. The substrate decanal and the end-products NAD<sup>+</sup> and capric acid had no effect on the light kinetics. The Michaelis constants of bacterial luciferase for FMNH

and decanal were  $3 \times 10^{-6} \text{M}$  and  $8 \times 10^{-7} \text{M}$ , respectively, and those of oxidoreductase for FMN and NADH were  $6.1 \times 10^{-6} \text{M}$  and  $1.6 \times 10^{-5} \text{M}$ , respectively.

375. Lee, John (1982). Sensitization by Lumazine Proteins of the Bioluminescence Emission from the Reaction of Bacterial Luciferases. *Photochem. Photobiol.* 36:689-697.

Lumazine protein from *Photobacterium phosphoreum* blue shifts the *in vitro* bioluminescence spectra in the reactions using each of the four main types of bacterial luciferases: *P. phosphoreum*, *P. leiognathi*, *Vibrio harveyi* and *V. fischeri*. For the reaction initiated with FMNH<sub>2</sub> and tetradecanal at 20°C, this "sensitizing" property of lumazine protein differs quantitatively between the luciferases. An interaction constant characterizing each type of luciferase may be derived from a reciprocal plot of the spectral shift against the lumazine protein concentration. The weakest interaction constant is in the *V. fischeri* reaction, 180  $\mu\text{M}$ . For the *V. harveyi* reaction the interaction is in the range of 6 to 9  $\mu\text{M}$ , and for both *Photobacterium* reactions it is 2 to 3  $\mu\text{M}$ . A concentration of only 0.6  $\mu\text{M}$  of lumazine protein is sufficient to cause an observable change in the *Photobacterium* bioluminescence spectra. For the *V. harveyi* case the interaction constant is near to the equilibrium  $K_d$  for the luciferase-lumazine protein complex, observed directly by Visser and Lee. Both constants are decreased markedly by increase in phosphate concentration so that it is concluded that, with *V. harveyi* luciferase, sensitization occurs within this protein-protein complex. For *P. phosphoreum* luciferase, however, the equilibrium complex is too weak to correspond to the sensitizing interaction and it is concluded that the rate-limiting process is a protein-protein bimolecular collision. As judged from their molecular weight around 20,000, spectral properties and ability to blue shift the bioluminescence spectra, lumazine proteins are identified in a second strain of *P. phosphoreum* and in *P. leiognathi*.

376. Lee, John (1985). The Mechanism of Bacterial Bioluminescence. In *Chemi- and Bioluminescence*, John G. Burr, ed., New York: Marcel Dekker, Inc., pp. 401-437.

The hypothesis that bacterial bioluminescence operates by a "sensitized chemiluminescence" mechanism is proposed. Although all luminous bacteria apparently share the same mechanism for

light emission, there are large species and strain differences in quantum yield and emission spectrum. The *in vivo* emission spectrum frequently differs from the *in vitro* spectrum. The "sensitized chemiluminescence" model proposes to explain this difference by postulating transfer of energy from the product of the exergonic chemical step in the chemiluminescent reaction to some other molecule in the system, which then functions as the *in vivo* emitter. This behavior is similar to that of the bioluminescent system in the sea pansy, *Renilla*. In bacteria, this "sensitizer" or "acceptor" molecule is called "lumazine protein." Lumazine protein has been isolated from four strains and two species of luminous bacteria and characterized. The observed variations in the protein can account entirely for the spectral shifts observed in the bacterial light emission. Emission intensities are reported for four bacterial species: *Vibrio harveyi*,  $2 \times 10^{14}$  photons/mL-min; *V. fischeri*,  $6 \times 10^{14}$  photons/mL-min; *Photobacterium phosphoreum*,  $0.6 \times 10^{14}$  photons/mL-min; and *P. leiognathi*,  $18 \times 10^{14}$  photons/mL-min.

377. Lee, John, Dennis J. O'Kane and Antonie J. W. G. Visser (1985). Spectral Properties and Function of Two Lumazine Proteins from *Photobacterium*. *Biochemistry* 24:1476-1483.

The spectral properties are compared for two 6,7-dimethyl-8-ribityllumazine proteins from marine bioluminescent bacteria, one from a psychrophile, *Photobacterium phosphoreum*, and the other from a thermophile, *Photobacterium leiognathi*. The visible spectral properties, which are the ones by which the protein performs its biological function of bioluminescence emission, are almost the same for the two proteins: at 2°C and 50 mM P<sub>i</sub> pH 7, fluorescence quantum yield  $\phi_f = 0.59$  and 0.54, respectively; fluorescence lifetime  $\tau = 14.4$  and 14.8 nsec, respectively; fluorescence maxima, both 475 nm; absorption maximum, 417 and 420 nm, respectively; circular dichroism minima at around 420 nm, both  $-41 \times 10^3 \text{ deg cm}^2 \text{ dmol}^{-1}$ . The ligand binding sites therefore must provide very similar environments and arguments are presented that the bound ligand is relatively exposed to solvent. The dissociation equilibrium was studied by steady-state fluorescence polarization. The thermophilic protein binds the ligand with  $K_d(20^\circ\text{C}) = 0.016 \mu\text{M}$ , 10 times more tightly than the other protein [ $K_d(20^\circ\text{C}) = 0.16 \mu\text{M}$ ]. The origin of the binding difference probably resides in

differences in secondary structure. The tryptophan fluorescence spectra of the two proteins are different, but more significant is an observation of the decay of the tryptophan emission anisotropy. For the psychrophilic lumazine protein this anisotropy decays to zero in 1 nsec, implying that its single tryptophan residue lies in a very "floppy" region of the protein. For the other protein, the anisotropy exhibits both a fast component and a slow one corresponding to rotation of the protein as a whole. This suggests that in the thermophilic protein the tryptophan region is held more rigidly. In both proteins, however, the ligand exhibits no independent mobility, as its rotational correlation time (respectively 19.5 and 17.5 nsec, 2°C) corresponds to the rotation of a sphere of hydrated M<sub>r</sub> approximately equal to 30,000.

378. Lee, John, E. Duane Small, Y.-M. Liu and S. Sinha (1979). High Molecular Weight Blue Fluorescence Protein from the Bioluminescent Bacterium *Photobacterium fischeri*. *Biochem. Biophys. Res. Comm.* 86(4):1241-1247.

A blue fluorescence protein has been purified from extracts of the bioluminescent bacterium *Photobacterium fischeri* and found to have a native molecular weight of 70,000 and to be a dimer of two identical subunits. SDS gel electrophoresis distinguishes the monomer from the two nonidentical subunits of luciferase. The molecular weight for this blue fluorescence protein contrasts with the much lower value (22,000) reported for the same type of protein isolated from *Photobacterium phosphoreum*.

379. Leis, Jeffrey M. and Suzanne Bullock (1986). The Luminous Cardinalfish *Siphamia* (Pisces, Apogonidae): Development of Larvae and the Luminous Organ. In *Proc., 2nd Int. Conf. on Indo-Pacific Fishes*, T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura, eds., Ichthyological Society of Japan, Tokyo, pp. 703-714.

Development of larval *Siphamia versicolor* was described from specimens 2.0-15.0 mm in length from plankton samples. Larvae were characterized by a bacterial luminous organ, a supraoccipital spine and extensive preopercular spination. Development of the luminous organ was studied by light and transmission electron microscopy. The organ develops from the gut and migrates forward. In the smallest larvae it has melanin bodies scattered at the periphery, a lumen,

and microvilli, but apparently lacks bacteria. During the pelagic larval period, the organ becomes heavily sheathed by melanin and packed with symbiotic, presumably luminescent bacteria. The larvae are unique among apogonids in head spination and pigment, as well as in the light organ, but share some characters with an as yet unidentified apogonid larva.

380. Leisman, Gary B. (1981). Yellow Light Emission in Marine Luminous Bacteria via a Yellow Fluorescent Protein. Ph.D. Dissertation, University of California, San Diego.

*Vibrio fischeri* strain Y-1, in contrast to all other luminous bacteria, emits yellow light in vivo with an emission maximum at 545 nm and a shoulder at 500 nm below 20°C. Above 24°C light emission is blue, while at 22°C light emission is a mixture of yellow and blue. A yellow fluorescent protein is responsible for this emission through a nonradiative energy transfer mechanism. This mechanism and factors that affect it are described.

381. Leisman, Gary, Daniel H. Cohn and Kenneth H. Nealson (1980). Bacterial Origin of Luminescence in Marine Animals. *Science* 208:1271-1273.

Bacterial luciferase activity was detected in light organ extracts of squids, fishes and pyrosomes, suggesting that these systems are derived from bacteria-animal symbioses. In none of these cases was it possible to culture luminous bacteria. Analyses of the decay kinetics show that the luciferases from the squid, ceratioid and pyrosome light organs are all similar to bacterial luciferases from the genus *Photobacterium*, while those from the anomalopid light organs are different.

382. Leisman, Gary and Kenneth H. Nealson (1979). Yellow Light Emission by Bacterial Extracts. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 70.

**ABSTRACT.** The discovery of a strain of *Photobacterium fischeri* that emits light with a peak of 545 nm and a shoulder at 490 nm if grown below 21°C is announced. The emission peak shifts to 490 nm if the cells are grown at 22-24°C; no yellow emission is produced if grown above 25°C in vivo. Crude enzyme extracts assayed in vitro show similar shifts. Dilution causes a blue spectral shift, reversible upon re-concentration. Partially purified luciferase emits only blue light.

383. Leisman, Gary and Kenneth H. Nealson (1982). Characterization of a Yellow Fluorescent Protein from *Vibrio (Photobacterium) fischeri*. In *Flavins and Flavoproteins*, pp. 383-386, Vincent Massey and Charles H. Williams, eds., New York: Elsevier North Holland, Inc. (*Dev. Biochem.* 21:383-386).

A yellow fluorescent protein has been isolated from a yellow-emitting strain of *Vibrio fischeri*. This protein participates by energy transfer in the production of the yellow light in a manner analogous to the participation of lumazine protein in the blue shift of light emission in vivo from *Photobacterium phosphoreum*. The physical and optical properties of the protein are described and its role in the yellow shift of the light emission is demonstrated.

384. Leisman, Gary and Kenneth H. Nealson (1982). Yellow Bioluminescence In Vivo from the Luminous Bacteria. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 302-313.

While most luminous bacteria emit light in the spectral range from 470 to 505 nm, a strain of *Vibrio fischeri* is reported with peak emission at 545 nm and a shoulder at 500 nm in vivo, but a maximum at 500 nm in vitro. The color is growth-temperature dependent, with no yellow luminescence occurring at 25°C, and the peak emission steadily shifting to yellow as the growth temperature is lowered toward 17°C.

385. Leisman, Gary and Frederick I. Tsuji (1981).  $K^+/Na^+$  Triggered Bioluminescence in the Oceanic Squid *Symplectoteuthis*. *Fed. Proc.*, 40(6):1659.

**ABSTRACT.** Bright light emission followed by long-lasting decay is stimulated in the large luminous organ of *Symplectoteuthis* by  $K^+$ ,  $Na^+$ ,  $Rb^+$ ,  $Cs^+$  and  $NH_4^+$  in decreasing order of effectiveness, but not by  $H^+$ ,  $Li^+$ , or  $Ca^{2+}$ . The decay consists of two components with different decay constants and oxygen is required. Stimulable light emission appears to depend on a specific cation gradient across a membrane.

386. Leisman, Gary and Frederick I. Tsuji (1981). Preliminary Report on the Mechanism of Bioluminescence in the Oceanic Squid *Symplectoteuthis*. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A.

DeLuca and William D. McElroy, eds., Academic Press, New York, pp. 709-714.

Studies on cell-free extracts of light organs from the squid *Symplectoteuthis oualaniensis* showed that potassium ion strongly stimulated light emission and that oxygen was absolutely required for the reaction. pH changes had little effect. A two-component decay, suggesting the existence of two light-emitting species, was observed. The essential reaction components appeared to be membrane-bound.

387. Levin, L. A., R. N. Utyushev, A. S. Artemkin, Yu. V. Chugunov and V. V. Ermakov (1982). Methods and Equipment for the Investigation of Occurrence of Bioluminescence in the Ocean. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. Woodland Hastings, eds., Akad. Nauk USSR, Krasnoyarsk, pp. 89-100.

Bathyphotometers may excite bioluminescence actively, by means of a pumping system, or passively, by means of their own motion through oceanic water. In the latter, the rate of movement determines the level of excitation and screening of the photodetector against external light is required. Screening may be accomplished by a "slot" method, which depends upon ambient light being reflected many times off the semiabsorbent surface of a series of bars, that also act as the stimulus for bioluminescence, or, more effectively, by a "rotor" method, which consists of a series of rotors along the axis of the bathyphotometer with their blades angled to the axis and opposed to the blades of the previous rotor. In addition to providing shielding, the movement of the blades stimulates bioluminescence. The "rotor" method is the basis of bathyphotometers currently in use.

388. Levine, Leonard D. and William W. Ward (1980). Isolation and Characterization of the Green-Fluorescent Protein and Photoprotein of *Phialidium gregarium*. *Abstr., Amer. Soc. Photobiol. 8th Ann. Meet.*, p. 48.

**ABSTRACT.** A green-fluorescent protein (GFP) isolated from the hydrozoan medusa *Phialidium gregarium* has a fluorescence emission spectrum similar in shape to those of *Aequorea* and *Renilla* but significantly blue-shifted, with peak emission at  $497 \pm 2$  nm. The excitation spectrum and molecular weight more closely resemble those of *Renilla* GFP

than *Aequorea* GFP. The *P. gregarium* photoprotein has a molecular weight of 23,000 and a pH profile for calcium-stimulated bioluminescence centered between pH 6 and 9.

389. Levine, Leonard D. and William W. Ward (1982). Isolation and Characterization of a Photoprotein, "Phialidin" and a Spectrally Unique Green-fluorescent Protein from the Bioluminescent Jellyfish *Phialidium gregarium*. *Comp. Biochem. Physiol.* 72B(1):77-85.

A calcium-activated photoprotein, "phialidin" and a green-fluorescent protein (P-GFP) have been isolated from the bioluminescent hydrozoan jellyfish, *Phialidium gregarium* and purified 170-fold and 500-fold, respectively. Phialidin has a mol wt of 23,000  $\pm$ 4% by gel filtration and a pH profile for calcium-stimulated bioluminescence between 6 and 9.5. It is less sensitive than aequorin, however, to low levels of calcium. With regard to mol wt (57,000  $\pm$ 4%) and thermal stability ( $T_m$  = 69°C), *Phialidium* GFP more closely resembles *Renilla* GFP than *Aequorea* GFP. The corrected fluorescence emission spectrum of P-GFP resembles those of *Renilla* and *Aequorea* GFP in shape; but, having a peak emission at 497 nm, it is unique among all known GFPs.

390. Lieberman, Stephen H. (1985). Small Scale Vertical Variability in Underwater Light Transmission, Bioluminescence and Chemical Properties in the Western Mediterranean and Greenland Sea. *EOS* 66(51):1320.

**ABSTRACT.** Small scale vertical variability in light attenuation, stimulated bioluminescence, temperature, salinity, pH and chlorophyll a fluorescence have been compared and interpreted in terms of the vertical stability of the water column.

391. Lieberman, Stephen H., David Lapota, Jon R. Losee and Alberto Zirino (1987). Planktonic Bioluminescence in the Surface Waters of the Gulf of California. *Biol. Oceanogr.* 4(1):25-46.

Continuous underway shipboard measurements of stimulated planktonic bioluminescence, chlorophyll a fluorescence and sea-surface temperature were made along a transect paralleling the north-south axis of the Gulf of California. Satellite-derived infrared imagery of sea-surface temperature was collected during the

same time period. Over large spatial scales (>10 km), bioluminescence was inversely correlated with sea-surface temperature. Bioluminescence levels were higher in the cooler waters of the northern and central gulf and lower in the warm waters of the southern gulf. Values ranged over three orders of magnitude ( $10^7$  -  $10^{10}$  photons  $\text{sec}^{-1} \text{cc}^{-1}$ ). Chlorophyll showed considerable patchiness and was not correlated with bioluminescence over large spatial scales. Over small spatial scales (<10 km), enhanced levels of bioluminescence were correlated with thermal fronts and regions of high chlorophyll.

392. Lieberman, Stephen H. and Alberto Zirino (1983). Planktonic Bioluminescence, Temperature, Chlorophyll Relationships in the Surface Waters of the Norwegian Sea. *EOS* 64(52):1102.

**ABSTRACT.** On a cruise in the Norwegian Sea in April, 1983, bioluminescence over large spatial scales was related to characteristics of different water masses. Small scale patchiness in bioluminescence intensity and chlorophyll fluorescence was correlated with gradients in sea surface temperature.

393. Losee, Jon R. (1982). Bioluminescence: Measurements and Organisms in the Upper 600 m. Progress Report Abstracts, Office of Naval Research, December, pp. 29-30.

**ABSTRACT.** Bioluminescence was measured to a depth of about 600 m on two dives on a moonless night in June, 1982, near the western edge of the Gulf Stream using two bathyphotometers, one open and one closed, mounted on the forward frame of the submersible Johnson Sea Link II. Surface light was detected to 200 m and obscured bioluminescence above 150 m in the open bathyphotometer. The bioluminescence maximum was observed at 120 m in the closed bathyphotometer. Below 200 m little activity was observed, with a small layer at 330-360 m. Examination of collected samples showed large numbers of dinoflagellates of several genera above 40 m, with rapid numerical dropping below 40 m. Copepod density was greatest at 20 m and dropped to 150 m. The copepod density profile was very similar to the closed bathyphotometer bioluminescence profile. Migrating layers at 275 m and 400 m appeared to consist mostly of copepods. The probably luminescent siphonophore *Vogtia serrata* was collected at 400 m. At this depth a bright

luminous display could be stimulated by a pulse from a flashlight. This effect diminished in shallower depths and disappeared by 60 m.

394. Losee, Jon R. and David Lapota (1981). Bioluminescence Measurements in the Atlantic and Pacific. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis, Minnesota: Burgess Publishing Co., pp. 143-152.

Bioluminescence intensity at the surface and to depths of 100 m is measured using a newly designed pumping system using 120-m-long hose intakes. A weak correlation with the thermocline is observed. Average intensities remain relatively constant, varying only by an order of magnitude at the surface or at a given depth, regardless of location. Higher average intensities are reported for nearshore bays, possibly due to higher nutrient concentrations. The number of flashes decreases rapidly below 50 m. Spectral measurements show an average peak emission at about 480 nm, with a small ultraviolet component in some cases between 350 and 400 nm.

395. Losee, Jon R. and David Lapota (1982). Ultraviolet Bioluminescence in the Marine Environment. *EOS* 63(45):944.

**ABSTRACT.** A small ultraviolet (wavelengths shorter than 400 nm) component is observed in situ in bioluminescence emissions from marine surface waters. This emission does not correlate with the broad spectrum and is not reproducible in the laboratory. It appears to correlate with the presence of luminous dinoflagellates and can be stimulated only once each night per organism.

396. Losee, Jon R. and David Lapota (1983). Laboratory Observations of Ultraviolet Bioluminescence from a Colonial Radiolarian. *EOS* 64(52):1102.

**ABSTRACT.** A small ultraviolet component (wavelengths shorter than 400 nm) has often been observed in bioluminescence in marine surface waters, but has never been observed in organisms tested in the laboratory. The problem may lie in the trauma associated with capturing and isolating the luminous organisms. On a cruise in the Norwegian Sea in April-May 1983, colonial radiolarians (similar to *Collozoum*) were maintained in filtered seawater for between a few hours and two days before testing. Under these conditions an ultraviolet component

representing less than 0.1% of the total broadband light emission per flash was observed.

397. Losee, Jon R., David Lapota, Mark L. Geiger and Stephen H. Lieberman (1984). Bioluminescence in the Marine Environment. In *Ocean Optics VII* (SPIE Vol. 489). Marvin A. Blizard, ed., Society for Photo-Optical Instrumentation Engineers, Bellingham, WA, pp. 77-98.

The Naval Ocean Systems Center and the Naval Oceanographic Office have been making measurements of bioluminescence in conjunction with other oceanographic parameters in surface waters (upper 200 m) and to depths of 3650 m using submersible vehicles. Biological samples and laboratory measurements of individual organisms' flash signatures are also obtained. Pumped/closed (closed in this text signifies light baffled) detectors are routinely used for surface and depth measurements of bioluminescence. An open (open signifies viewing directly out into the seawater) system is used in conjunction with a pumped detector for deep dives. A brief overview of the instrumentation, some examples of data obtained and conclusions based on measurements are presented.

398. Losee, Jon R., David Lapota and Stephen H. Lieberman (1985). Bioluminescence in Diverse Oceanic Regions. *EOS* 66(51):1320.

**ABSTRACT.** Bioluminescence in the upper 100 m of the water column is primarily due to small plankton and is often associated with changes in physical oceanographic parameters, especially temperature, light transmission and chlorophyll fluorescence. Measurements of these parameters in the Gulf of California, North Atlantic, North Pacific, Mediterranean Sea and Indian Ocean show that bioluminescence as a function of depth in frontal and upwelling regions generally correlates with temperature and anticorrelates with light transmission. Short-term variance depends on organism type and abundance.

399. Losee, Jon R., David Lapota and Stephen H. Lieberman (1985). Bioluminescence: A New Tool for Oceanography. In *Mapping Strategies in Chemical Oceanography* (Advances in Chemistry Series No. 209). Alberto Zirino, ed., Baltimore (Maryland): American Chemical Society, pp. 211-234.

Because bioluminescence in marine surface waters (upper 100 m) is primarily due to small plankton, it can be successfully characterized by relatively simple photometer systems. The two basic types of bioluminescence detectors are an open type that views directly out into the seawater and a closed type that views a closed volume through which seawater is pumped. The bioluminescence variability is an interdependent phenomenon often associated with changes in physical and chemical parameters. For example, ocean frontal regions are almost always associated with enhanced levels of bioluminescence. Bioluminescence spectral content and signal kinetics often indicate the type of organisms present.

400. Losee, Jon R., David Lapota and Stephen H. Lieberman (1987). Bioluminescence: Spatial Statistics in the North Atlantic. *EOS* 68(50):1695.

**ABSTRACT.** Bioluminescence has been measured at 5 m depth on a transect from Copenhagen, Denmark, to Wilmington, NC. Nighttime bioluminescence was 10 times greater than daytime bioluminescence. Coherent structure in near-shore and North Atlantic current waters was seen on scales down to about 3 km. In central gyre waters no structure was seen on scales to 160 km. Thus in the central gyre and on scales less than 3 km in near-shore waters, patches are limited to less than 0.6 km, randomly distributed and non-overlapping.

401. Lümme, Peter and Ulrich K. Winkler (1986). Bioluminescence of Outer Membrane Defective Mutants of *Photobacterium phosphoreum*. *FEMS Microbiol. Lett.* 37(3):293-298.

Mutants of *Photobacterium phosphoreum* NCMB7 hypersensitive to several antimicrobial agents were independently isolated and characterized. The hypersensitivity was probably due to changes in the outer membrane (OM) structure; the electrophoretic lipopolysaccharide profile of one mutant was altered. In addition, two mutants exhibited elevated cell surface hydrophobicity. With respect to bioluminescence, the mutants were dim or dark, and showed strongly reduced activities of the inducible enzymes luciferase and fatty-acid reductase. Our results suggest that the outer membrane is involved in the regulation of bacterial bioluminescence.

402. Lümme, Peter and Ulrich K. Winkler (1987). Outer Membrane Structure Is Important for

Bioluminescence in *Photobacterium phosphoreum*. In *Bioluminescence and Chemiluminescence: New Perspectives*, J. Schölerich, R. Andreeson, A. Kapp, M. Ernst and W. G. Woods, eds., New York: John Wiley and Sons, pp. 591-594. (Abstract published in *J. Bioluminescence Chemiluminescence* 1(2):117, 1986).

In mutants of *Photobacterium phosphoreum* hypersensitive to oxacillin, in vivo bioluminescence and the activities of luciferase and myristic acid reductase, both inducible enzymes, are greatly reduced. This fact suggests that the structural integrity of the outer membrane is a prerequisite for bioluminescence. However, luminescence in a mutant strain resistant to tetracycline is not affected. Thus the 33K major protein, which presumably forms hydrophilic pores with the outer membrane, does not appear to be essential for autoinducer transport.

403. Lynch, Richard V. (1980). Bioluminescence in and near the Arabian Sea. Naval Research Laboratory Letter Report 4351-78.

Literature on bioluminescence around the Arabian Sea is reviewed and briefly summarized.

404. Lynch, Richard V. (1980). Problems and Opportunities Connected with Marine Biological Phenomena. In *Advanced Concepts in Ocean Measurements for Marine Biology*, Ferdinand P. Diemer, F. John Vernberg and Donna Z. Mirkes, eds., Columbia (South Carolina): University of South Carolina Press, pp. 245-255.

The word "phenomenon" means anything apparent to the senses that can be scientifically measured. In a laboratory, phenomena can be isolated from one another and individually studied. In the ocean, individual phenomena undergo complex synergistic and antagonistic interactions, making isolation difficult. In fact, understanding of biological dynamics requires understanding of the interactions. The gathering of the large amounts of data needed to study these interactions requires new methods of measurement. Remote sensing can provide fast and repeated coverage of large areas and offers the possibility of sensing several variables simultaneously. Automated instruments can make long-term measurements at selected sites with minimum attention. Data processing using computers offers a way of analyzing and storing all these data, which is less cumbersome than individual analysis. The variety

and quantity of knowledge required to study large-scale processes suggests the use of a multidisciplinary team approach. The advantages of this approach and of using the new means of measurement are outlined in three examples of current biological interest—pollution studies, hot spots, and bioluminescence.

405. Lynch, Richard V. (1980). Bioluminescence in the World's Oceans. In *Naval Research Laboratory Review*, pp. 70-73.

The seasonal and geographic distribution of marine bioluminescence and naval programs to study it are discussed. This article is a condensed version of "Patterns of Bioluminescence in the Oceans," Naval Research Laboratory Report 8475 by Richard V. Lynch in 1980.

406. Lynch, Richard V. (1981). Patterns of Bioluminescence in the Oceans. Naval Research Laboratory Report 8475.

Bioluminescence occurs throughout the world's oceans at all times of year. However, the possibilities of encountering it vary according to location and season. Maps indicating these possibilities are presented in this report, along with a discussion of their reliability and the statistical problems involved in their construction and interpretation.

407. Lynch, Richard V. (1981). The Distribution of Luminous Marine Organisms: A Literature Review. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis, (Minnesota): Burgess Publishing Co., pp. 153-159.

This article reviews the literature on spatial and vertical distribution of bioluminescence observations and bioluminescent organisms and the short-term temporal variations and discusses instrumental measurement problems and possible correlations with environmental parameters. The literature on luminous displays is also reviewed.

408. Lynch, Richard V. (1982). Bioluminescence in and near the Arctic Ocean. Naval Research Laboratory Letter Report 4350-80.

Literature on bioluminescence in high northern latitude seas is reviewed and briefly discussed.

409. Lynch, Richard V. (1985). Detection of Bioluminescence Stimulated by Aircraft Using

Explosive Charges. Naval Ocean Research and Development Activity, Stennis Space Center, MS. Technical Note 311.

Horizontal distribution studies of bioluminescence are impaired due to slow, inaccurate sampling techniques. Rapid aerial surveys lack statistical validity because it is impossible to distinguish between an absence of bioluminescence due to absence of organisms or due to an absence of stimulation. This report deals with one method of stimulating bioluminescence by means of explosive charges dropped from an aircraft. Such charges are ineffective in stimulating bioluminescence for aerial survey purposes because the aircraft cannot maintain the point of impact within the camera field of view.

410. Lynch, Richard V., William R. Hemphill and Arnold F. Theisen (1983). Use of Fraunhofer Lines to Detect Remotely Bioluminescence in Daylight. Naval Research Laboratory Activity Report 8759.

Bioluminescence has been detected against a background of strong sunlight using Fraunhofer lines. Luminous dinoflagellates in scotophase were agitated by pouring or stirring during a brief exposure (about 1.5 min) to sunlight while being imaged using a Fraunhofer line discriminator (FLD) set to 486.1 nm. Steadily glowing luminescent bacteria were also examined. Computer enhancement of the resulting data showed bioluminescence easily detectable and distinguishable despite a high background of solar light.

411. Lynch, Richard V. and Arthur V. Stiffey (1986). An Overview of Basic Bioluminescence Research at NORDA. In *The NORDA Review*: Naval Ocean Research and Development Activity, Stennis Space Center, MS, pp. 137-144.

Bioluminescence occurs throughout the world's oceans at all times of the year and at every depth. In some regions it creates spectacular displays. It can be stimulated in a number of ways—notably mechanically, chemically, photically, barometrically and, possibly, acoustically. Most naval research has concentrated on mechanical stimulation because movement will stimulate the organisms to flash or glow. NORDA research has also concentrated on vertical distribution of bioluminescence in the water column, on correlations with physical and chemical parameters in seawater and on stimulation and quenching mechanisms. A correlation between

bioluminescence and temperature gradients has been established. Lasers and small pressure pulses have been used successfully to stimulate bioluminescence in dinoflagellates. Studies of chemical effects on bioluminescence have led to the development of assay techniques with many potential applications. Instrumentation development is being promoted to enhance naval capabilities in oceanography.

412. Mackie, George O. and Claudia E. Mills (1983). Use of the *Pisces IV* Submersible for Zooplankton Studies in Coastal Waters of British Columbia. *Can. J. Fish. Aquat. Sci.* 40:763-776.

This study evaluates the usefulness of a small submersible for observations of the plankton. A method for calculating plankton densities from estimates of mean interanimal distances is described. Estimates made by this method were compared with estimates based on net sampling and were found to be in fair general agreement with them. Fragile gelatinous forms were better counted from the submersible, small organisms by netting. Some delicate species, known to be abundant from submersible observations, were never recognized in net samples. Submersible observations also gave important insights into vertical distribution of the plankton. Several species were found to exist within unexpectedly narrow and sharply defined layers, often at densities greatly surpassing density estimates based on net samples. In Saanich Inlet, B.C., plankton distribution was studied in relation to the seasonal formation and dispersion of the oxygen-deficient basin water. Other data deal with behavior, color change, bioluminescence and vertical migration of planktonic organisms. They conclude that submersible observations are potentially valuable in plankton research and make recommendations regarding instrumentation and observer training as an aid in planning future dives.

413. Makemson, John C. (1986). Luciferase-Dependent Oxygen Consumption by Bioluminescent Vibrios. *J. Bacteriol.* 165(2):461-466.

Oxygen uptake due to luciferase in two luminous *Vibrio* species was estimated in vivo by utilizing inhibitors having specificities for luciferase (decanol) and cytochromes (cyanide). Cyanide titration of respiration revealed a component of oxygen uptake less sensitive to cyanide which was completely inhibitable by low concentrations of decanol. From this it was estimated that in vivo luciferase is

responsible for less than 12% (*Vibrio harveyi*) or 20% (*Vibrio fischeri*) of the total respiration. From these data in vivo bioluminescent quantum yields are estimated to be not lower than 1.7 and 2.6% respectively.

414. Makemson, John C. and J. Woodland Hastings (1979). Glutamate Functions in Osmoregulation in a Marine Bacterium. *Appl. Environ. Microbiol.* 38(1):178-180.

*Benecke harveyi* growing in either minimal or complex media increased the total amino acid pool with increasing salinity of the medium. Glutamate was the predominant amino acid involved.

415. Makemson, John C. and J. Woodland Hastings (1979). Inhibition of Bacterial Bioluminescence by Pargyline. *Arch. Biochem. Biophys.* 196(2):396-402.

Pargyline (N-benzyl-N-methyl-2-propynylamine), an inactivator of mitochondrial monoamine oxidase, inhibits growth and in vivo and in vitro bioluminescence in *Benecke harveyi*. The inhibition is competitive with the two substrates, FMNH and aldehyde, and the inhibitor binds with a reaction intermediate of the enzyme luciferase to form a stable, but reversible, adduct. Inhibition of in vivo bioluminescence is an apparently complex phenomenon and may involve a block in the synthesis of aldehyde.

416. Makemson, John C. and J. Woodland Hastings (1979). Poising of the Arginine Pool and Control of Bioluminescence in *Benecke harveyi*. *J. Bacteriol.* 140(2):532-542.

Arginine dramatically stimulates bioluminescence in the marine bacterium *Benecke harveyi* growing in minimal media, an effect that is due to increases in both the synthesis and expression of luciferase. To elucidate the mechanism of this phenomenon, studies were made of the transport and metabolism of arginine in *B. harveyi*. The transport of arginine and lysine involves two kinetically distinct transport systems for the uptake of arginine and lysine. In contrast, ornithine is transported only by a system common to all three amino acids. The internal amino acid pools were measured in mutants that do not show stimulation of bioluminescence by arginine and in wild-type cells that do. In minimal media, the internal arginine pools are undetectably low. Furthermore, exogenously added labeled arginine is rapidly

transported and converted to citrulline and argininosuccinate. The results can be accommodated by a model in which the internal arginine is poised at a very low concentration; the stimulatory effect of exogenous arginine on luciferase biosynthesis occurs at the transcriptional level and the actual mediator can be either arginine or arginyl transfer ribonucleic acid.

417. Makemson, John C. and J. Woodland Hastings (1982). Iron Represses Bioluminescence and Affects Catabolite Repression of Luminescence in *Vibrio harveyi*. *Current Microbiol.* 7:181-186.

Bioluminescence and the synthesis of luciferase in *Vibrio harveyi* growing in a minimal medium are repressible by iron; this is not significantly reversed by cyclic adenosine 3',5'-monophosphate (cAMP). Cultures grown with added iron emit less light and possess less luciferase per cell than those grown under conditions of limiting iron; this may have significance in relation to the function of luciferase as an electron carrier. With iron and with glycerol as the sole carbon and energy source, the addition of glucose causes further repression, both transient and permanent and this is only partially reversible by cAMP. Without iron, glucose addition results in only a small and transient repression, but this is fully reversible by cAMP. The inability of cAMP to reverse iron-influenced repression may be explained by both a low rate of transport of cAMP into the bacteria and increased intracellular levels of cyclic nucleotide phosphodiesterase.

418. Makemson, John C. and J. Woodland Hastings (1984). Luciferase Dependent Growth of *Vibrio harveyi*. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 84:137.

**ABSTRACT.** Experiments on *V. harveyi* in different media showed that reduced growth rates are apparently coupled to a decrease in cytochrome content. Growth rate inhibition under these conditions may be partially alleviated by the synthesis and activity of bacterial luciferase.

419. Makemson, John C. and J. Woodland Hastings (1986). Luciferase-Dependent Growth of Cytochrome-Deficient *Vibrio harveyi*. *Microbiol. Ecol.* 38:79-85.

The presence of  $10^{-6}$  M human serum transferin (TF) in a minimal medium retarded the growth of

*Vibrio harveyi* and inhibited the synthesis of cytochromes and stimulated the development of bioluminescence. The addition of  $10^{-7}$  M arginine to the TF medium further stimulated bioluminescence and increased the growth rate of the bacteria. These data suggest that luciferase, functioning as a terminal oxidase, supported the growth of such cytochrome-deficient bacteria.

420. Makiguchi, Nobuyoshi, Masanobu Arita and Yoshiyuki Asai (1979). Isolation, Identification and Several Characteristics of Luminous Bacteria. *J. Gen. Appl. Microbiol.* 25(6):387-396.

To apply bioluminescence of luminous bacteria to industrial use, isolation of luminous bacteria from various sources was carried out on the basis of strong light intensity and 18 strains were obtained. Eleven of these strains were identified as *Photobacterium phosphoreum* and seven as *Vibrio fischeri*. Maximum light intensities of these isolates were quite different among strains tested and two stock cultures of luminous bacteria supplied by the American Type Culture Collection had a very poor bioluminescence compared to the new isolates. Bioluminescent emission spectra from the two isolated strains were fairly different from each other, indicating the possibility of obtaining luminous bacteria which could emit light of different colors. While cultivation of some luminous bacteria was repeated several times in a liquid medium, decrease of light intensity was observed. By spreading the culture broth on an agar plate medium, three kinds of colonies were observed. They were quite different in the appearance of colonies and maximum light intensity. These results suggest that the occurrence of dim mutants in liquid cultures is disadvantageous for maintaining the light intensity constant and a strain which could be as stable as possible at this point should be used for industrial purpose.

421. Makiguchi, Nobuyoshi, Masanobu Arita and Yoshiyuki Asai (1980). Application of a Luminous Bacterium to Fish-Attracting Purpose. *Bull. Jap. Soc. Scientific Fisheries* 46(11):1307-1312.

In order to apply the bioluminescence of luminous bacteria to the fishing industry, studies on the attracting effect of a luminous material containing immobilized luminous cells and a luminous raw bait attached with luminous cells on various kinds of fish were carried out. Water tank experiments showed that

the luminous material had an attracting effect on freshwater shrimp *Palaemon paucidens*, but on the contrary, apparent evading effect on parrot fish *Oplegnathus fasciatus*. Fishing ground experiments revealed that the luminous material had an attracting effect on king crab *Paralithodes camtschaticus* caught with a trap, squid as well as prawn *Penaeus orientalis* caught by trawl fishing, neither an attracting nor an evading effect on crab *Chionoecetes opilio* caught with a trap, and a distinct evading effect on shrimp *Pandalus borealis* caught with a trap. Fishing ground experiments also showed that the luminous raw bait attached with luminous cells had a tremendous effect on bottom fishing by which grunt, gopher, dorado, scorpionfish, mullet, flatfish and shark were caught, and the number of caught fish was 4.8 times larger than that of the control. In addition, the luminous raw bait seemed to have some attracting effect on tuna caught with tuna long lines and the number of caught tuna was 1.2 times larger than that of the control.

422. Makiguchi, Nobuyoshi, Masanobu Arita and Yoshiyuki Asai (1980). Optimum Cultural Conditions for Strong Light Production by *Photobacterium phosphoreum*. *J. Gen. Appl. Microbiol.* 26(2):75-83.

Strong light intensity of the culture broth and industrially feasible cultural conditions are required in order to apply the bioluminescence of luminous bacteria to attracting fish. To obtain strong bioluminescence of the culture broth, studies of the optimum cultural conditions for strong light production by *Photobacterium phosphoreum* MT-10201 were carried out. Strong light intensity of the culture broth was obtained at an initial NaCl concentration in the medium between 3% and 5.5%, starting pH 8.5 and cultivation temperature 20°. The addition of 0.1% malic acid to the medium resulted in enhanced light intensity of the culture broth but mannose, arginine, dodecylaldehyde and phosphate buffer used for pH control during cultivation had no effect. Cultivation of the luminous bacterium in 2-L and 20-L fermentors was carried out and luminous raw bait was prepared successfully by using the culture broth directly as a luminous source.

423. Malkov, Yu. A. and V. S. Danilov (1985). Non-Heme Iron in Reaction of Bacterial Luciferase from *Vibrio fischeri*. *Stud. Biophys.* 105(2):115-120.

The experiments provide evidence for a functional iron requirement of bacterial luciferase,

using a specific chelating agent, o-phenanthroline. The reducing agents NAD(P)H and dithionite are found to affect the formation of the complex  $Fe^{2+}(OP)_2$ . The iron of bacterial luciferase exists largely in the oxidized form and its reduction is dependent on the presence of FMN. The amount of luciferase in the case where that of iron 1 mole/mole of enzyme appeared to be much lower in comparison with the data earlier reported for luciferase.

424. Malkov, Yu. A. and V. S. Danilov (1986). Effect of Ethylenediaminetetraacetate on Bacterial Luciferase. *Biochemistry (USSR)* 51(4): 622-626 (Russian); 536-540 (English).

The effect of EDTA on the activity of luciferase from the luminescent bacteria *Photobacterium (Vibrio) fischeri* was studied. EDTA was found to be a reversible inhibitor. The inhibition is due to the chelation of the nonheme iron of the enzyme. A study of the effect of hydrophobic chemical compounds on bacterial bioluminescence showed that EDTA can sharply distort the nature of the interaction of luciferase with an aliphatic aldehyde. At the same time, the presence of EDTA in buffer solutions significantly increases the stability of the enzyme.

425. Malkov, Yu. A., V. S. Danilov, and N. S. Egorov (1981). The Effect of Inhibitors of Mixed-Function Oxidases on Bacterial Bioluminescence. *Appl. Biochem. Microbiol.* 18(1):76-80 (Russian); 66-70 (English).

An investigation was made of the influence of the specific cytochrome P-450 inhibitors metyrapone (2-methyl-1,2-di-3-pyridyl-1-propanone) and SKF 525-A (2-diethylaminoethyl-2,2-diphenyl valerate) on bioluminescence of the bacteria *Photobacterium fischeri* and on a purified preparation of bacterial luciferase. Both compounds effectively quench bacterial bioluminescence. Kinetic analysis of the luminescence reaction stimulation by the substrates FMNH<sub>2</sub> and aldehyde permitted the conclusion that the inhibition mechanism is the same for both compounds. Metyrapone and SKF 525-A prevented aldehyde binding strictly concurrently but nonconcurrently inhibited the reaction relative to FMNH<sub>2</sub>. The data obtained are in good agreement with the idea of the participation of cytochrome P-450 as a terminal component of bacterial luciferase.

426. Mallefet, J. and Fernand Baguet (1984). Oxygen Consumption and Luminescence of *Porichthys* Photophores Stimulated by Potassium Cyanide. *J. Exp. Biol.* 109:341-352.

Isolated photophores of *Porichthys notatus*, maintained in saline at 20°C, do not luminesce and show an oxygen consumption rate of  $0.07 \pm 0.01$  nmol min<sup>-1</sup> photophore<sup>-1</sup>. In the presence of  $10^{-6}$  m-KCN, the photophores do not luminesce but the resting respiration decreases by about 50%. In the presence of  $10^{-5}$  m-KCN, some photophores do not luminesce and their respiration rate decreases by about 75%. Others show a response and resting oxygen consumption slowly increases. At high concentration ( $10^{-6}$  m and  $10^{-3}$  m), KCN induces a large light emission and increase in oxygen consumption. The stimulatory effect of KCN on the photophore oxygen consumption is tentatively explained by an activation of the luciferin-luciferase system by calcium ions.

427. Mallefet, J. and Fernand Baguet (1985). Effects of Adrenalin on the Oxygen Consumption and Luminescence of the Photophores of the Mesopelagic Fish *Argyrops leucogymnus*. *J. Exp. Biol.* 118:341-349.

Photophores isolated from the mesopelagic fish *Argyrops leucogymnus* consume oxygen at a rate of  $1.22 \pm 0.17$  nmol min<sup>-1</sup> in saline at 20°C. In the presence of  $5 \times 10^{-6}$  molL<sup>-1</sup> adrenalin the preparations that responded by a long-lasting luminescence showed a significant decrease of their resting respiration rate. After the adrenalin had been washed out, oxygen consumption increased immediately to the previous resting level and was inhibited by  $5 \times 10^{-4}$  molL<sup>-1</sup> KCN. It is suggested that the mechanism of light production by isolated photophores of the epipelagic fish *Porichthys* and the mesopelagic fish *Argyrops leucogymnus* are different.

428. Mallefet, J. and Fernand Baguet (1986). Oxygen Consumption and Luminescence of *Maurolicus* Photophores Stimulated by Potassium Cyanide. *J. Exp. Biol.* 126:469-477.

Isolated photophores of *Maurolicus muelleri*, maintained in saline at 20°C, consume oxygen at a mean rate of  $1.25 \pm 0.07$  nmol O<sub>2</sub> min<sup>-1</sup> (N=50). In the presence of  $5 \times 10^{-6}$  molL<sup>-1</sup> KCN, seven preparations did not luminesce while two showed only dim luminescence. In all nine preparations, the resting oxygen consumption decreased by about 50%. In the

presence of  $5 \times 10^{-5}$  molL<sup>-1</sup> KCN, all of the photophores produced a slow, low luminescence and their oxygen consumption decreased by about 75%. In the presence of  $5 \times 10^{-4}$  molL<sup>-1</sup> KCN, all of the photophores produced a slow, high luminescence and their oxygen consumption decreased rapidly by about 92%. It is suggested that the oxygen needs for light production by the isolated photophores of the mesopelagic fish, *Maurolicus*, differ from those of the epipelagic fish, *Porichthys*.

429. Mankovskiy, V. I., V. L. Vladimirov and O. V. Martynov (1980). The Time and Space Variability of Optical Properties of Water Masses in the FGGE Region. *Morsk. Gidrofiz. Issledov.* (Sevastopol) 80(2):131-140. (Russian).

The results of complex hydrooptical research in the region are analyzed. Vertical profiles of the radiation attenuation coefficient, bioluminescence intensity, and chlorophyll fluorescence, the depth of Secchi disk visibility, and the color index of the water are measured. The variability of the above parameters in space and time is described and its relation with that of hydrological parameters is shown.

430. Marine Observer, The (1924-present). Various titles and authors.

Special mention must be made of this journal, published quarterly by the British Meteorologic Office. In "The Marine Observers' Log" almost every issue contains anecdotal observations of bioluminescence by ships' personnel, taken from ships' logs. Often fascinating and always informative, these accounts have been entirely omitted from this bibliography due to lack of room.

431. Marra, John (1984). BIOWATT: A Study of Bioluminescence and Optical Variability in the Sea. Lamont-Doherty Geological Observatory of Columbia University, Palisades, NY.

This document reviews the scientific issues in ONR's BIOWATT program and outlines the effort to resolve those issues.

432. Marra, John and Eric O. Hartwig (1984). Biowatt: A Study of Bioluminescence and Optical Variability in the Sea. *EOS* 65(40):732-733.

The rationale, goals and history of the Biowatt program of the Office of Naval Research are given. The kinds of experiments to be performed and their

position in the program are described. The overall schedule and a specific schedule of cruises are provided. A light budget for the Sargasso Sea, based on preliminary measurements, is suggested.

433. Martin, Normand and Michel Anctil (1984). Luminescence Control in the Tube-Worm *Chaetopterus variopedatus*: Role of Nerve Cord and Photogenic Gland. *Biol. Bull.* 166(3):583-593.

Electrical and mechanical stimulation of the parapodial epidermis of *Chaetopterus variopedatus* evoked luminescence which was propagated only slightly to adjacent ipsilateral, but not to contralateral, parapods. In contrast, electrical stimulation of the highly modified aliform notopods led to propagation of luminescence through the entire body. Above a critical stimulus threshold, stimulation of the ventral nerve cord at any level evoked luminescence which was through-conducted. Only stimulation of the cerebral ganglia could bring about an orderly antero-posterior sequence of luminescence propagation. Discharges of nerve cord impulses invariably preceded the onset of spontaneous or electrically stimulated luminescence, and the propagation of both activities was interrupted by section of the nerve cord. Mechanical stimulation of parapods also evoked impulses at the corresponding level in the nerve cord. A large photogenic gland lying on the dorso-median surface of the 10-12th segments was refractory to electrical and mild mechanical stimulation, but responded by releasing large amounts of luminescent mucus after rupture of its epithelium. Mechanical agitation of the tube was quickly followed by the ejection of a cloud of luminescent mucus through one end, and readjustment of the worm's position to the other end of the tube. Epithelial luminescent activities are coordinated by the ventral nerve cord and luminescent discharges from the photogenic gland appear to be associated with defensive and tube cleaning activities.

434. Matheson, Ian B. C. and John Lee (1981). An Efficient Bacterial Bioluminescence with Reduced Lumichrome. *Biochem. Biophys. Res. Comm.* 100 (2):532-536.

Photoreduced lumichrome reacts in vitro with oxygen in the presence of tetradecanal and a specially purified sample of bacterial luciferase selected for minimum fluorescence at 490 nm upon 350 nm excitation from *Vibrio harveyi* yielding a rapidly

decaying bioluminescence with an emission maximum at 476 nm. This emission is spectrally similar to the fluorescence spectrum of oxidized lumichrome. Less purified luciferase samples possessing appreciable fluorescence in the 490 nm region invariably gave bioluminescence at 490 nm. These results are interpreted in terms of an energy transfer mechanism.

435. Matheson, Ian B. C. and John Lee (1982). A New Protein-Protein Reaction Mechanism for In Vitro Bacterial Bioluminescence. *Abstr. Amer. Soc. Photobiol. 10th Ann. Meet.*, p. 182.

**ABSTRACT.** At 2°C bioluminescence of *V. harveyi* luciferase with FMNH<sub>2</sub> and tetradecanal reaches maximum intensity in 1.5 s and exhibits a three-component decay. The fluorescence takes several minutes to reach maximum and exhibits first-order decay kinetics. Excess aldehyde alters the reaction kinetics. These results suggest that two chemically energized species, one non-fluorescent and the other a fluorescent transient, provide the energy for the bioluminescent reaction, with aldehyde concentration controlling their relative proportions. Lumazine proteins may substitute for the fluorescent transient. A model for the reaction is proposed.

436. Matheson, Ian B. C. and John Lee (1983). Kinetics of Bacterial Bioluminescence and the Fluorescent Transient. *Photochem. Photobiol.* 38(2):231-240.

The addition of FMNH<sub>2</sub> to *Vibrio harveyi* luciferase at 2°C in the presence of tetradecanal results in the formation of a highly fluorescent transient species with a spectral distribution indistinguishable from that of the bioluminescence. The bioluminescence reaches maximum intensity in 1.5 s and decays in a complex manner with exponential components of  $10^{-1} \text{ s}^{-1}$  and  $7 \times 10^{-4} \text{ s}^{-1}$ . The fluorescent transient rises exponentially at  $7 \times 10^{-2} \text{ s}^{-1}$  and decays at  $3 \times 10^{-4} \text{ s}^{-1}$ . The slowest bioluminescence component, comprising the bulk of the bioluminescence, decays at twice the rate of the fluorescent transient under all variations of reaction conditions: concentration of reactants, temperature 2-20°C and aldehyde chain length—decanal, dodecanal, and tetradecanal. The activation energy for both the slowest bioluminescence decay and the transient fluorescence decay is  $80 \text{ kJ} \cdot \text{mol}^{-1}$ . An energy transfer scheme is proposed to explain the results where two distinct chemically energized species utilize

the fluorescent transient as emitter for the slower bioluminescences and for the faster process a fluorophore present in the protein preparation. Kinetic observations suggest that typical preparations of *V. harveyi* luciferase comprise 15% active protein.

437. Matheson, Ian B. C., John Lee and Franz Müller (1981). Bacterial Bioluminescence: Spectral Study of the Emitters in the In Vitro Reaction. *Proc., Nat. Acad. Sci. US* 78(2):948-952.

Transient fluorescent species are observed in the bioluminescent reactions of three reduced flavin mononucleotides with aliphatic aldehydes and oxygen, catalyzed by bacterial luciferase. In each case the fluorescence spectral distribution is similar to that of the bioluminescence but is readily distinguishable from it on the basis of a significantly greater signal strength. The corrected bioluminescence maxima using *Benecke harveyi* luciferase are 479 nm (iso-FNMFH), 490 nm (FMNH<sub>2</sub>) and 560 nm (2-thio-FMNH<sub>2</sub>). In an ethanol glass at 77 K, 2-thioriboflavin is fluorescent ( $\phi_F = 0.03$ ,  $\lambda_{max} = 562$  nm). These results are interpreted by a sensitized chemiluminescence mechanism in which the flavins bound to luciferase act as acceptors of excitation energy. For 2-thio-FMNH, this acceptor species appears to be the oxidized 2-thio-FMN on the basis of the spectral evidence, whereas for the other flavins, some form of reduced species is a more likely candidate.

438. Matheson, Ian B. C., John Lee and E. F. Zalewski (1984). A Calibration Technique for Photometers. In *Ocean Optics VII*, Marvin A. Blizard, ed., Vol. 489, Society of Photo-Optical Instrumentation Engineers, pp. 380-381.

The quantum yield of the luminol reaction is remeasured using a silicon photodiode detector and a geometry for which the light collection efficiency is known absolutely. The luminol reaction is used in turn to calibrate a portable photometer of similar geometry which may be used to calibrate underwater photometers in conjunction with a transferrable light-emitting fluid. Luminous bacteria, especially *Photobacterium phosphoreum*, in liquid medium are as useful as that fluid.

439. McCapra, Frank (1978). The Chemistry of Bioluminescence. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 49-73.

Theories of the chemistry of excited states and energy transfer reactions are discussed and applied to bioluminescence. Various models of chemical mechanisms are presented. A chemical basis for understanding bioluminescence reactions is established and research problems in bacterial bioluminescence are outlined.

440. McCapra, Frank (1982). The Chemistry of Bioluminescence. *Proc., R. Soc. London* B215:247-272.

The study of the mechanisms of bioluminescence is described from the standpoint of organic chemistry. An outline of the occurrence and function of the phenomenon is given and the knowledge acquired by the organic chemist is set in this context.

441. McConnaughey, Fred (1980). Fireflies under the Sea. *Oceans* 13(4):8-11.

The story of the rediscovery of *Kryptophanaron alfredi*, a flashlight fish related to *Photoblepharon* and *Anomalops* but last seen in 1907, is told. The fish lives in the Caribbean Sea, especially near the Cayman Islands, at depths of about 600 feet, but rises to 100 feet at night to feed. A related species, *Kryptophanaron harveyi*, has also been found in the Gulf of California.

442. McCosker, John E. and Richard H. Rosenblatt (1987). Notes on the Biology, Taxonomy, and Distribution of Flashlight Fishes (Beryciformes: Anomalopidae). *Jap. J. Ichthyol.* 34(2):157-164.

New information concerning the distribution and biology of anomalopid fishes is presented. There are five valid described species: *Anomalops katoptron* and *Photoblepharon palpebratus*, widely distributed in the central and western Pacific Ocean; *P. steinitzi* from the Red Sea and Comoro Islands; *Kryptophanaron alfredi* from the Caribbean; and *K. harveyi* from Baja California. *P. steinitzi* differs from *P. palpebratus* in coloration, head bone ornamentation, and pelvic ray number. The second known specimen of *K. harveyi* is described in detail. The occurrence of large specimens of *Anomalops* in deep water and small specimens in shallow water is discussed. Synonyms and a key to the species of anomalopids are provided.

443. McFall-Ngai, Margaret J. (1981). New Function for the Teleost Gas Bladder: A Source of Oxygen for

the Bioluminescent Bacteria in the Leiognathid Light Organ. *Abstr., Western Soc. Naturalists 62nd Ann Meet.* 62:31.

**ABSTRACT.** Bacterial bioluminescence requires considerable oxygen, yet ultrastructural and histological analyses of the light organ of leiognathid fishes indicate that the blood supply is poor. The gas bladder, however, is separated from the light organ only by a thin membrane, the guanine content of which is low compared to the remainder of the gas bladder lining. Guanine is known to act as an oxygen barrier to prevent uncontrolled diffusion of gases into the surrounding tissues. It has also been found that the gas bladder contains a gas mixture enriched to about 23% oxygen. These two findings suggest that the gas bladder serves as a source of oxygen for the light organ bacteria.

444. McFall-Ngai, Margaret J. (1983). Adaptations for Reflection of Bioluminescent Light in the Gas Bladder of *Leiognathus equulus* (Perciformes: Leiognathidae). *J. Exp. Zool.* 227(1):23-33.

The gas bladder of leiognathid fishes functions not only in buoyancy but also in reflection of bioluminescent light from the circumesophageal light organ. Purine distribution, quality (guanine/hypoxanthine ratio) and concentration, as the basis for reflectivity, were assayed enzymatically for different portions of the gas bladder lining of the common leiognathid, *Leiognathus equulus* (Forsk.). For highly reflective areas, the percentage of tissue wet mass and dry mass represented by purine was also determined. The results indicate that total purine content in the reflective areas of the leiognathid bladder was significantly higher than values determined for other similar, shallow water fishes; instead, purine content in these reflective areas was similar to that known for very deep-dwelling fishes, in which heavy purine deposition is correlated with high pressures and high oxygen concentrations in the bladder. In addition, the results show that differential purine distribution within the bladder correlates strikingly with the path of bioluminescent light. The dorsal bladder lining, the primary site of incident luminescence, had extremely high purine concentrations (averaging 2.80 mg/cm<sup>2</sup>), whereas the secondary reflective surfaces, the lateral (1.81 mg/cm<sup>2</sup>) and ventral (1.22 mg/cm<sup>2</sup>) portions, although high in purine content, had concentrations significantly lower than the dorsum. Areas through which light is

transmitted, the light organ-bladder interface (0.9 mg/cm<sup>2</sup>) and the posterior region (0.19 mg/cm<sup>2</sup>), were greatly reduced in purine content. The enhancement of purine in the reflective portions of the bladder and the correlation of the differential distribution of purines with the path of light indicate that the *L. equulus* gas bladder is exquisitely adapted to function as a reflector of bioluminescent light.

445. McFall-Ngai, Margaret J. (1983). The Gas Bladder as a Central Component of the Leiognathid Bacterial Light Organ. *Amer. Zool.* 23(4):907.

**ABSTRACT.** Leiognathid fishes maintain a symbiotic luminous bacterium, *Photobacterium leiognathi*, in a circumesophageal light organ adnate to the gas bladder. The gas bladder acts both as a differential reflector-transmitter of bacterial light and as a source of oxygen for the luminescent system of the light organ bacteria.

446. McFall-Ngai, Margaret J. (1983). Patterns, Mechanisms, and Control of Luminescence in Leiognathid Fishes. Ph.D. Dissertation. University of California, Los Angeles.

Leiognathid fish responded to increases and decreases of ambient light intensity with increases and decreases of ventral luminescent output, but in decreasing ratio to the ambient light intensity as it increased. In addition, the ventral luminescence was heterogeneous rather than even over the ventrum, with the brightest spots just behind the gills. These patterns suggest "disruptive illumination" rather than "counterillumination" as one of a number of camouflaging mechanisms. The gas bladder was the primary reflector of the internally produced light. *Gazza minuta* exhibited a high degree of versatility of luminescent behavior. Sexual dimorphism of the light organ system was observed in a number of leiognathid species and suggests bioluminescent signalling in reproductive behavior.

447. McFall-Ngai, Margaret J. and Paul V. Dunlap (1983). Three New Modes of Luminescence in the Leiognathid Fish *Gazza minuta*: Discrete Projected Luminescence, Ventral Body Flash and Buccal Luminescence. *Mar. Biol.* 73:227-237.

Three new modes of luminescence are described for *Gazza minuta* (Bloch) (Perciformes: Leiognathidae) as observed in specimens collected in the Philippines in April and May, 1982: Discrete projected

luminescence (DPL), ventral body flash and buccal luminescence. DPL sharply contrasts with previously reported modes of diffuse luminescence in leiognathids (counterillumination and opercular flash) in being a pair of bright collimated beams of light emanating from the fish in an anteroventral direction. The brightness, coherence, directionality and control of DPL suggest striking similarities to luminescence in anomalopid (flashlight) and monocentrid (pinecone) fishes and perhaps in certain apogonids (cardinalfishes). The structural correlate for DPL is a small clear patch of skin lying at the posterior margin of each opercular cavity. Luminescence from the internally located light organ traverses transparent bone and translucent muscle before passing through the clear skin of the patch area. Behavioral and anatomical observations of ventral body flash and buccal luminescence are also presented. These new modes of luminescence indicate a much greater than expected diversity of luminescent behaviors in leiognathids, perhaps greater than that of any other organism yet studied. The internal location of the light organ is recognised as providing the potential for this diversity.

448. McFall-Ngai, Margaret J. and Paul V. Dunlap (1984). External and Internal Sexual Dimorphism in Leiognathid Fishes: Morphological Evidence for Sex-Specific Bioluminescent Signaling. *J. Morphol.* 182:71-83.

Fourteen species of leiognathid fishes (Perciformes, Leiognathidae) from the Philippine Islands, Thailand, Japan, Indonesia, and Palau were examined for accessory secondary sexual dimorphism. Thirteen species exhibit either external dimorphism (a clear patch of skin on the flanks of males, a large clear patch of skin on the opercular margins of males, or a flank stripe in males) or internal dimorphism (large light organs in males) or both. Eight of the 14 species (and possibly as many as 11) exhibit both forms of sexual dimorphism. Two species show only internal light organ volume dimorphism, and one species shows neither external nor internal dimorphism. Sexual dimorphism is thus very common in leiognathids. The externally dimorphic skin patches are closely associated with the internally dimorphic light organ system in seven species (and possibly as many as ten), indicating a potential for light emission through the clear patches. A bioluminescent signaling function by males is therefore suggested for the sexual

dimorphism in leiognathids, which may play an important role in the schooling behavior as well as in species and sexual recognition of these coastal fishes.

449. Medvedeva, S. Ye. (1984). Morphology and Ultrastructure of Luminescent Bacteria. In *Luminescent Bacteria* (English translation of *Sveryashchiviesya Bakterii*, Ye. N. Kondrat'yeva, ed., Izdatel'stvo "Nauka," Moscow), pp. 70-97. JPRS-UBB-85-018-L, 31 Oct 1985.

The morphology and ultrastructure of several species of luminous bacteria are described and changes under different culture conditions are noted. Luminescence is found to be associated with electron-dense osmiophilic cytoplasmic inclusions.

450. Medvedeva, S. Ye. and M. V. Salnikov (1982). Morphology and Ultrastructure of Marine Luminous Bacteria. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., *Akad. Nauk USSR*, Krasnoyarsk, pp. 213-226.

The morphology and ultrastructure of several species of luminous bacteria are described and changes under different culture conditions are noted. Luminescence is found to be associated with electron-dense osmiophilic cytoplasmic inclusions.

451. Meighen, Edward A. (1979). Biosynthesis of Aliphatic Aldehydes for the Bacterial Bioluminescent Reaction. Stimulation by ATP and NADPH. *Biochem. Biophys. Res. Comm.* 2487(4):1080-1086.

Although the activity of bacterial luciferase is dependent on the presence of a long chain aliphatic aldehyde as well as FMNH<sub>2</sub> and O<sub>2</sub>, the mechanism of biosynthesis of aliphatic aldehydes in bioluminescent bacteria is not yet known. The present paper reports the stimulation of luminescence by ATP and NADPH on injection of FMNH<sub>2</sub> into extracts of *Photobacterium phosphoreum* containing no added aldehyde. Over a 300-fold stimulation of luminescence was observed after incubation of the extract for 10 min with NADPH and ATP, increasing to 500-fold if myristic acid was also present. These results provide evidence in vitro for the existence of an enzyme dependent on ATP and NADPH and capable of synthesizing the aliphatic aldehydes necessary for bacterial luminescence.

452. Meighen, Edward A. and Irene Bartlett (1980). Complementation of Subunits from Different Bacterial

Luciferases. Evidence for the Role of the  $\beta$  Subunit in the Bioluminescent Mechanism. *J. Biol. Chem.* 255(23):11,181-11,187.

Complementation of the nonidentical subunits ( $\alpha$  and  $\beta$ ) of luciferases isolated from two different bioluminescent strains, *Beneckea harveyi* and *Photobacterium phosphoreum*, has resulted in the formation of a functional hybrid luciferase ( $\alpha_h \beta_p$ ) containing the  $\alpha_p$  subunit from *B. harveyi* luciferase ( $\alpha_p$ ) and the  $\beta$  subunit from *P. phosphoreum* luciferase ( $\beta_p$ ). The complementation was unidirectional; activity could not be restored by complementing the  $\alpha$  subunit of *P. phosphoreum* luciferase with the  $\beta$  subunit of *B. harveyi* luciferase, showing that the subunits from these luciferases were not identical. Kinetic parameters of the hybrid luciferase reflecting the intermediate and later steps of the bioluminescent reaction as well as the overall activity and specificity were essentially identical to the same kinetic parameters for *B. harveyi* luciferase, the source of the  $\alpha$  subunit, and quite distinct from those of *P. phosphoreum* luciferase. However, kinetic parameters that reflected the initial step in the reaction involving interaction of FMNH<sub>2</sub> and luciferase were altered in the hybrid luciferase compared to both the parental luciferases, the K<sub>d</sub> for FMNH<sub>2</sub> actually being closer to that observed for the *P. phosphoreum* luciferase (the source of the  $\beta$  subunit). These results provide direct evidence that modification or alteration of the  $\beta$  subunit in a dimeric luciferase molecule can affect the kinetic properties and indicate that the  $\beta$  subunit plays a functional role in the bioluminescent mechanism. It is proposed that both the  $\alpha$  and  $\beta$  subunits are involved with the initial interaction with FMNH<sub>2</sub>, whereas subsequent steps in the mechanism are dictated exclusively by the  $\alpha$  subunit and are unaffected by alteration in the  $\beta$  subunit.

453. Meighen, Edward A., Denis Riendeau and Andrew Bognar (1981). Bacterial Bioluminescence: Accessory Enzymes. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*. Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 129-137.

NADH:FMN oxidoreductases in *Beneckea harveyi* have been demonstrated and may interact with luciferase, but are not under the same regulation as luciferase and are not induced with it. However, an aldehyde dehydrogenase is cosynthesized with

luciferase and appears to regulate aldehyde levels for the bioluminescent reaction. In *Photobacterium phosphoreum* an aldehyde reductase may play this role, but it is not yet clear. In either case a fatty acid reductase, specific for catalyzing the reduction of tetradecanoic acid to aldehyde, is coincuded with luciferase.

454. Mezhevikin, V. V., Ye. S. Vysotskiy and V. V. Zavoruev (1984). Metabolic and Structural Organization of Luminescence System of Luminous Bacteria. In *Luminescent Bacteria* (English translation of *Svetyashchiyessa Bakterii*, Ye. N. Kondrat'yeva, ed., Izdatel'stvo "Nauka," Moscow), JPRS-UBB-85-018-L, 31 October 1985, pp. 190-216.

The metabolic pathways of synthesis of various substrates in the bacterial bioluminescence reaction are discussed. Emphasis is placed on identification of the aldehyde factor, the enzymes involved its synthesis, and its precursors, and on the nature and reduction mechanism of the native analogue of FMN involved with luciferase (and possibly other proteins as well) as the light emitter. A general plan of organization of the luminescence system is presented along with kinetic and intensity data under various reaction conditions. The physicochemical properties of some of the enzymes comprising the system are given. The link between the basal cell metabolism and the luminescence system and regulation of luminescence are explored. The possibilities of several repression and inhibition schemes as means of regulating cell growth and light emission while in symbiosis within light organs in higher organisms are discussed.

455. Mezhevikin, V. V., V. V. Zavoruev and E. S. Visotsky (1981). Extraction and Some Properties of the "Aldehyde Factor" from Luminous Bacteria. *Izv. Sib. Otd. Akad. Nauk SSSR Ser. Biol. Nauk* 81(3):49-53 (Russian).

Decreasing the time of lysis, along with additional operations, greatly increases the residual capacity of bacterial extracts to luminesce without added aldehyde. By comparison of the properties of long chain aliphatic aldehydes and the bacterial "aldehyde factor" according to their involvement in the luminescent reaction in vitro, the aldehyde factor is tentatively identified with lauric aldehyde in *Photobacterium leiognathi* strain 54 and with myristic aldehyde in an unidentified psychrophilic bacterium strain 151.

456. Mikkelsen, Paula M. (1987). The Euphausiacea of Eastern Florida (Crustacea: Malacostraca). *Proc. Biol. Soc. Wash.* 100(2):275-295.

Twenty-eight species of euphausiacean crustaceans are recorded from off the eastern Florida coast, from collections by the University of Miami and Harbor Branch Foundation, Fort Pierce. *Thysanopoda cristata*, *T. pectinata*, *Nematobrachion sexspinosus* and *Stylocheiron robustum* are newly recorded for the area. Species bibliographies and a key to adult specimens are presented, along with taxonomic and ecological notes.

457. Millam, Gary (1984). Tripping the Light Fantastic. *Oceans* 17(4):3-8. Also published in *Anchor Line* 1985 (9):no page numbers.

A popular account of the phenomenon of bioluminescence is given. Luminous displays are described, along with luminescence and its possible functions in various marine organisms. Experiments supporting the hypothesis of counterillumination are discussed in some detail. The chemistry of the simplest reaction is outlined and applications are discussed, in particular remote sensing of ships and fish schools and pollution monitoring.

458. Miron, Marie-José, Luc LaRivière, Jean-Marie Bassot and Michel Anctil (1987). Immunohistochemical and Radioautographic Evidence of Monoamine-Containing Cells in Bioluminescent Elytra of the Scale-Worm *Harmothoe imbricata* (Polychaeta). *Cell Tissue Res.* 249:547-556.

Elytra of the scale-worm *Harmothoe imbricata* were examined for the presence of monoamine-like immunoreactivities and radioautographic reactions. Serotonin (5-HT)-like immunoreactivity was widely distributed among the cellular constituents of the elytra, being present in epithelial cells including photocytes, in elytral nerves, clear cells and the loose neuronal plexus of the middle compartment. The distribution of [<sup>3</sup>H]5-HT labelling coincided with that of the immunoreactivity except for an additional reactive band extending through the upper cuticle layer. Tyrosine hydroxylase (TH)-like immunoreactivity was detected in epithelial cells, sensory papillae and elytral ganglion and nerves, with little or no staining in clear cells and plexus neurons of the middle compartment. Radioautographic labelling with [<sup>3</sup>H]noradrenaline and [<sup>3</sup>H]adrenaline overlaid many epithelial cells, elytral nerves and

sensory papillae, but not the loose neuronal plexus or, apparently, clear cells. It is concluded that monoaminergic systems are widely distributed and that they must play important roles as neuroactive and/or paracrine substances in the elytral neuroectoderm. The distribution of [<sup>3</sup>H]5-HT label in photocytes also suggests the involvement of serotonergic mechanisms in luminescence control, luminescence being the only known effector activity of elytra.

459. Morin, James G. (1979). Bioluminescence in the Hundred-Fathom Codling, *Physiculus rastrelliger* (Gadiformes, Moridae). *Abstr., West Soc. Naturalists 60th Ann. Meet.* 60:40-41.

**ABSTRACT.** Bioluminescence is first reported in the benthopelagic fish *Physiculus rastrelliger*. The light organ is located ventrally immediately anterior to the anus, communicates with the rectum via a duct and contains the luminous bacterium, *Photobacterium phosphoreum*. Light emission is controlled by chromatophores and can probably be dispersed over much of the ventral surface.

460. Morin, James G. (1981). Coastal Bioluminescence: Patterns and Functions. *Bull. Mar. Sci.* 33(4):787-817.

Individual bioluminescent organisms in coastal waters often occur in high densities, but the number of luminescent species is relatively low, about 1 to 2%. Simple emitting systems, involving either photocytes or photosecretion, tend to be the dominant luminescent types in coastal organisms. However, complex light organs, as either glandular light organs or photophores, occur among some of the fishes. This situation contrasts with oceanic regions where organisms with photophores tend to dominate. Most of the luminescent signals in coastal waters occur in response to contact stimulation as simple conspicuous fast flashes (<2 sec) or slow glows (>5 sec). It is suggested that most coastal luminescence functions to deter potential predation primarily by fast flashes, which repel a predator, or by slow glows, which attract a predator toward the decoy light and away from the prey. As a third antipredatory strategy, some fishes with glandular light organs produce a concealing luminescence so that their predators fail to detect them as prey. As a second major function, particularly among coastal fishes with glandular light organs, luminescence is used to obtain prey through attraction and/or detection. Thirdly, light may also be used for

communication between conspecifics, particularly for mating, aggregating and territorial purposes. Finally, luminescence might serve mutualistic (advertising) purposes as, for example, between luminous bacteria and visual consumers. The preponderance of simple luminescent systems present in comparatively few species in the photically complex and heterogeneous environments of coastal waters contrasts sharply with the majority of species in the more homogeneous photic environment of the midwaters of the open sea where photophores and complicated luminescent patterns dominate. Conversely, the complex photic regimen of the shallow oceans and terrestrial environments suggests distinct parallels might exist between communications using luminescence and those using ambient reflected light, which is characteristic of all other visual communication.

461. Morin, James G. (1981). Bioluminescent Patterns in Shallow Tropical Marine Fishes. *Proc., 4th Int. Coral Reef Symp.* 2:569-574.

Bioluminescence in shallow tropical marine fishes is mainly restricted to nocturnally active species which forage on small motile invertebrates, especially crustaceans. In these fishes, luminous organs are primarily either ocular light organs or, more commonly, gut-associated light organs. Very few shallow-water species produce light from dermal photophores. Ocular light organs are of the bacterial type and primarily function in attracting and detecting prey. Luminescence from gut-associated light organs is produced either from bacteria or from glands which contain *Cypridina*-like luciferin. The light from these gut-associated organs is usually expressed externally as a diffuse ventral glow. This glow, when it matches the characteristics of the downwelling ambient light, effectively camouflages the fish from any predators or prey which might be below. The more precise visual acuity of organisms in shallow water may account for the predominance of diffuse counterillumination among shallow water fishes compared to those of midwaters. In contrast to the diffuse luminescence of shallow-water fishes, most luminous midwater fishes have discrete ventral photophores. To the less visually acute organisms of the mesopelagic, this distribution of photophores may produce a counter illuminating effect similar to that seen in shallow-water fishes. The luminescent systems of all shallow-water luminous fishes may have evolved as a consequence of the dietary connection to crustacean prey; endogenous

systems may have arisen from a utilization of the luciferin synthesized by their crustacean prey (the *Cypridina*-like system) while bacterial systems may have arisen in conjunction with chitinase-producing luminous bacteria which aided in the digestion of crustacean exoskeletons.

462. Morin, James G. (1981). Bioluminescence among Tropical Marine Fishes. *Abstr., 4th Int. Coral Reef Symp.*, pp. 43-44.

**ABSTRACT.** Bioluminescence in shallow tropical marine fishes is limited to five families—Monocentridae, Anomalopidae, Leiognathidae, Apogonidae and Pempheridae. The first three are all luminous through symbiotic luminous bacteria. Apogonids are non-luminous, luminous through bacterial symbionts, or self-luminous. Pempherids are non-luminous or self-luminous. Bacterial symbionts are *Photobacterium fischeri*, *P. leiognathi* or unidentified. Control is exercised by a variety of means. Functions of the luminescence are multiple and complex.

463. Morin, James G. (1982). Multiple Communication Functions in Luminescent Marine Organisms. In *Abstr., AAAS Symposium on Biocommunication: New Discoveries and Ideas* (Abstr., Pap. Am. Assoc. Adv. Sci. Nat. Meet. 148:36), p.36.

**ABSTRACT.** Luminous organisms display complex spatial and temporal patterns of light emission often associated with intricate behavioral activities. The displays appear to function primarily for 1) avoiding predators; 2) obtaining prey; or 3) communication.

464. Morin, James G. (1986). "Firefleas" of the Sea: Luminescent Signaling in Marine Ostracode Crustaceans. *Fla. Entomol.* 69(1):105-121.

Caribbean ostracodes of the genus *Vargula* secrete luminescent emissions either as bright, long-lasting clouds or as complex trains of shorter, precisely spaced pulses. The large, bright clouds are generally produced during late twilight and have an effective antipredatory function. These emissions are similar among all species. Conversely, complex trains usually occur for a limited time just post-twilight in specific habitats within reef and seagrass systems. These train are species specific displays produced by males and are presumably directed toward sexually

receptive benthic (bottom dwelling) females. In most species, luminescing males are accompanied by silent satellite males. These swarms have characteristics of both leks and speers. There are three primary display patterns among the approximately 15 species observed: (1) about two-thirds of the species produce trains that progressively shorten, (2) about one quarter produce evenly spaced trains and (3) one species produces pulsed displays from multiple males. In most species, displaying males will usually synchronize their signals, by entrainment, with distantly signaling males. This synchronization produces a spectacular, reef-wide, sweeping luminescence that is reminiscent of a slow motion version of the flashing of synchronous fireflies from Southeast Asia. The reproductive patterns, life history and biological activities of these ostracodes, along with their unusual signaling patterns, suggest that there is strong male-male competition and probably female choice involved in their mating systems. They show interesting parallels and differences to various insect mating aggregations including fireflies, chorusing insects and insect swarms.

465. Morin, James G. and E. L. Bermingham (1980). Bioluminescent Patterns in a Tropical Ostracod. *Amer. Zool.* 20(4):851.

**ABSTRACT.** The ostracod *Vargula huxleyi* (identified correctly as *V. bullae* in Abstract Number 402 above) emerges from the reefs of St. Croix island about 50 min after sunset or just after moonset and initially, during predation by apogonids, produces a bright glow lasting >10 s, which may be interpreted as a defensive display. Following this period and lasting for about one hour, a sexual signalling display is initiated by the female in two forms, a "calling" display and a "mating" display. These repetitive display pulses are synchronized, presumably to effect mating while avoiding predation.

466. Morse, David, Patrice M. Milos, Etienne Roux and J. Woodland Hastings (1987). LBP Protein Exhibits a Circadian Rhythm but Its mRNA Does Not. Gordon Conf. on Chronobiology.

**ABSTRACT.** Circadian regulation of the cellular amounts of the luciferin binding protein (LBP) in *Gonyaulax* occurs at the translational level. LBP mRNA is invariant with time.

467. Morse, David, Patrice M. Milos, Etienne Roux and J. Woodland Hastings (1987). The Circadian Rhythm of Luciferin Binding Protein in *Gonyaulax* Depends on Translational Control. *Abstr., Cold Spring Harbor Laboratory Res. Conf.*

**ABSTRACT.** Circadian regulation of the cellular amounts of the luciferin binding protein (LBP) in *Gonyaulax* occurs at the translational level. LBP mRNA is invariant with time.

468. Morse, David, Patrice M. Milos, Etienne Roux and J. Woodland Hastings (1987). Luminescence Proteins Exhibit Circadian Rhythms but Their mRNAs Do Not. *Biol. Bull.* 173(3):568.

**ABSTRACT.** The substrate luciferin, the enzyme luciferase and the luciferin-binding protein, three components of the bioluminescent system in the dinoflagellate *Gonyaulax polyedra*, are under circadian control. However, levels of mRNA for luciferin binding protein and luciferase synthesis remain constant. These results indicate that circadian control of the protein amounts is at the translational rather than the transcriptional level.

469. Muntz, W. R. A. (1983). Bioluminescence and Vision. In *Experimental Biology at Sea*, A. G. Macdonald and I. G. Priede, eds., New York: Academic Press, pp. 217-238.

The bioluminescent emission spectra of four species from four phyla are graphed and compared with the transmission spectrum of Jerlov 1A water and the spectral absorbance and difference spectra of the retinas of four species of fish. The matches suggest that bright bioluminescence could be visible at distances of 50-170 m, depending on water type. The theory of countershading and other possible biological functions of bioluminescence are discussed. The presence of yellow eye lenses in several species of deep sea fish and squid is detailed. A theory that these lenses, by attenuating bioluminescence emissions less than downwelling light, are useful in breaking countershading camouflage, is advanced.

470. Nakamura, Takao, Takahide Watanabe, Kenzaburo Yoshida and Haruo Watanabe (1982). Mechanisms of Bacterial Bioluminescence. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. Woodland Hastings, eds. Krasnoyarsk: Akad. Nauk USSR pp. 179-194.

The chemical components, steps and pathways of the light-emitting reaction of *Photobacterium phosphoreum* are described and schematized. Enzyme turnover rates and electronic pathways are discussed. Changes in reaction kinetics, stoichiometry, spectral emission and absolute intensity under different environmental conditions are described.

471. Nawata, Tomoki and Takao Sibaoka (1979). Coupling Between Action Potential and Bioluminescence in *Noctiluca*: Effects of Inorganic Ions and pH in Vacuolar Sap. *J. Comp. Physiol.* A134(2):137-149.

The ionic dependency of the flash-triggering action potential (FTP) evoked across the vacuolar membrane in *Noctiluca* was studied by injecting various salt and pH buffer solutions into the vacuole. Electron microscopic observations showed that the peripheral cytoplasmic compartment sandwiched between vacuole and pellicle is  $0.1 \pm 0.07 \mu\text{m}$  in thickness, so that it has a very small volume. The resting membrane resistance and capacitance measured across the cell surface were about  $10 \text{ K}\Omega/\text{cm}^2$  and  $0.8 \mu\text{F}/\text{cm}^2$  respectively. Under normal conditions the FTP, which is 50-60 mV in amplitude, arises from a potential of -150 to -160 mV. More than tenfold increase in concentration of  $\text{K}^+$ ,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{NH}_4^+$ , or  $\text{SO}_4^{2-}$  in the vacuole produced no significant change in the amplitude of FTP. Injections of HCl-glycine buffer solutions of various pH were used to alter the intrinsic vacuolar pH (about 3.5) within the range of 2.5 to 3.7 without damaging the cells. The FTP amplitude rose about 58 mV per unit drop in pH. Crude aqueous extracts from the cells emitted light most effectively when the pH was lowered from 8.2 to 5.5. None of the other major cations found in the vacuole showed any effect on the light emission of the extract. From these findings, they propose a proton hypothesis explaining the coupling between the bioluminescence and the action potential.

472. Nawata, Tomoki and Takao Sibaoka (1986). Membrane Potential Controlling the Initiation of Feeding in the Marine Dinoflagellate, *Noctiluca*. *Zool. Sci. (Tokyo)* 3:49-58.

Feeding behavior of the unicellular marine alga *Noctiluca* is induced by replacing the normal artificial seawater (ASW) with  $\text{SO}_4^{2-}$  free ASW. Membrane potential changes were examined before and during the  $\text{SO}_4^{2-}$ -mediated feeding. *Noctiluca* cells show a

spontaneous, repeating transient potential change in the normal ASW. About 80% of the cells immersed in the  $\text{SO}_4^{2-}$  free ASW quickly stopped the spontaneous potential change, and then showed a long-lasting hyperpolarizing vacuolar potential (hVP). Feeding behavior appeared only when the hVP was -80 mV or more negative and lasted for a period of approximately 1 min or more. Both  $\text{Cl}^-$  (400 mM or more) and  $\text{Ca}^{2+}$  (1 mM or more) in the  $\text{SO}_4^{2-}$  free ASW were needed to induce the hVP and feeding behavior.  $\text{Mg}^{2+}$  did not affect the hVP, but the  $\text{SO}_4^{2-}$  free ASW of 20 mM  $\text{Mg}^{2+}$  or less failed to induce the feeding behavior. The other ions ( $\text{Na}^+$ ,  $\text{K}^+$  and  $\text{H}^+$ ) were not needed to induce the hVP and feeding behavior. Radiotracer experiments revealed that no significant increases in  $\text{Ca}^{2+}$  influx were found just before feeding behavior was induced, but both  $\text{Ca}^{2+}$  influx and efflux increased significantly in association with feeding. A possible ionic basis involved in the initiation of feeding is discussed.

473. Nealson, Kenneth H. (1979). Alternative Strategies of Symbiosis of Marine Luminous Fishes Harboring Light-Emitting Bacteria. *Trends Biochem. Sci.* 4:105-109.

Physiological analyses of luminous bacteria indicate that the different symbiotic species can be separated into two distinct physiological types. This division is based upon differences in (1) the responses of the bacteria to various oxygen tensions, and (2) the production of pyruvate by the bacteria. It is proposed, on the basis of these distinctions, that symbiosis must operate in fundamentally different ways in the two host-symbiont systems. Two models of symbiosis consistent with the known facts are presented and discussed.

474. Nealson, Kenneth H. (1982). Mechanisms of Bioluminescence: Kinetics-Spectral and Biochemical Properties as a Probe of Marine Communities and Interactions. In *ONR Oceanic Chemistry and Biology Group Program Science Report*, 1 March, pp. V-23-V-24.

**ABSTRACT.** A station capable of lowering an instrument package to a depth of 200 m and recording 1.5 samples per msec in each of 16 data channels has been erected over Scripps Canyon. A photometer designed to collect data on the temporal features of radiance due to bioluminescence and sunlight is about to be installed. Data from this instrument will be

compared to spectral and kinetic data recorded from individual luminous pelagic organisms in the laboratory and outputted as a 3-dimensional surface.

475. Nealson, Kenneth H. (1987). Bacterial Luminescence. In *McGraw-Hill Encycl. Sci. Technol.* (6th edition) 2:313.

The habitats of luminous bacteria and the biochemistry and physiology of their light emission, including control mechanisms such as autoinduction, are briefly presented. Experiments on gene cloning of the lux gene into *E. coli* are outlined.

476. Nealson, Kenneth H. and A. Charles Arneson (1985). Marine Bioluminescence: About to See the Light. *Oceanus* 28(3): 13-18.

A brief, popular review of bioluminescence is presented. Properties of bioluminescence in selected luminous marine groups are tabulated. Habitats, organisms and processes related to bioluminescence in the different marine zones are summarized. The chemistry, functions and control of bioluminescence in selected organisms is outlined. The Scripps Canyon moored, automated bioluminescence observation system is described and the possibility of identifying organisms by their bioluminescent "signature" (variations in flash spectra and kinetics) is discussed.

477. Nealson, Kenneth H., A. Charles Arneson and A. Bratkovich (1984). Preliminary Results from Studies of Nocturnal Bioluminescence with Subsurface Moored Photometers. *Mar. Biol.* 83:185-191.

Spatial and temporal patterns of bioluminescent flashes were recorded from fall 1982 through spring 1983 by photometers moored offshore in Scripps Canyon, La Jolla, California, USA. From depths between 8 and 90 m, real-time data were transmitted by cable to a laboratory on land approximately one mile (1.7 km) away. In addition, temperature, depth and current velocity and direction were monitored either in real time by direct coupling to a laboratory-based system, or by internal data storage systems that were retrieved at regular intervals and subsequently analyzed. Our studies showed that our field station is largely uncoupled from wave action effects usually associated with luminescence measurements made from ships. Bioluminescent activity varied greatly both during a single night and between different nights. Vertical profiling of the water column between 8 and 90 m showed evidence

of vertical migration, patchiness of distribution and large-scale spatial differences in total bioluminescent activity. Currents had a major impact on patterns of bioluminescent activity, however, sometimes high levels of luminescence were recorded in complete absence of currents. Diel cycles, organism patchiness, the level of downwelling ambient light and currents appeared to interact in controlling the levels and patterns of bioluminescence.

478. Nealson, Kenneth H., A. Charles Arneson and Michael E. Huber (1986). Identification of Marine Organisms Using Kinetic and Spectral Properties of Their Bioluminescence. *Mar. Biol.* 91:77-83.

They used a polychromator consisting of six photomultiplier tubes, each filtered to a different wavelength with narrow bandpass interference-filters, to study bioluminescence. Spectral and kinetic data collected from ten marine species in the laboratory describe their luminous flashes. These data suggest that the concept of luminous signatures, within the limits of our studies, is a valid one, with potential uses for future biological studies both in the laboratory and in situ. The kinetic parameters considered were rise time (RT), decay time (DT) and total time (TT), while the spectral parameters consisted of ratios of light intensities at 480 and 520 nm to the intensity at 500 nm. One-way analysis of variance (ANOVA) demonstrated significant heterogeneity among species for all variables. A posteriori analysis performed with the ANOVA for TT indicated that mean TT for most species is significantly different from all other species. Canonical discriminant analysis was performed to estimate the value of kinetic and spectral parameters for species identification. Kinetic data were somewhat more valuable in species classification than spectral data. Discriminant analysis with RT and DT alone gave 83.1% correct species-classifications. Classification based only on relative intensities at 480 and 520 nm was 77.5%. When all four variables were included, classification success was 100%.

479. Nealson, Kenneth H., Daniel Cohn, Gary Leisman and Bradley M. Tebo (1981). Co-Evolution of Luminous Bacteria and Their Eukaryotic Hosts. *Ann. N. Y. Acad. Sci.* 361:76-91.

The associations of three genera of luminous bacteria, *Photobacterium*, *Beneckea* and *Xenorhabdus*, with their hosts are tabulated. Criteria for the assessment of a true symbiotic relationship are

established. Chemical and kinetic criteria for distinguishing bacterial luciferase from other luciferases, and *Photobacterium* luciferase from those of *Benickea* and *Xenorhabdus* are given. Luminous bacteria may be found free-living in marine environments, saprophytically associated with decaying organic matter, living in animal guts, or associated with light organs. The only terrestrial luminous bacterium, *Xenorhabdus*, is associated with nematode guts. Most symbiotic relationships are extracellular, but some, namely with *Pyrosoma* and possibly other urochordates, are intracellular. Nonculturable luminous bacteria, such as those found in *Leiognathus elongatus*, anomalopid and ceratioidean fish, and heteroteuthid squid, may be a step toward intracellularity.

480. Nealson, Kenneth H. and J. Woodland Hastings (1979). Bacterial Bioluminescence: Its Control and Ecological Significance. *Microbiol. Rev.* 43(4):496-518.

The biochemistry and kinetics of the luminous reaction in bacteria are described. The taxonomic relationships among luminous and related nonluminous species are tabulated. Control mechanisms of both light emission and luciferase synthesis are discussed. The distribution of free-living forms in various habitats is given and saprophytes, parasites and commensal life styles and habitats are discussed in detail. Symbiosis in connection with light organs and functions of luminescence are explained.

481. Nealson, Kenneth H. and J. Woodland Hastings (1980). Luminescent Bacterial Endosymbionts in Bioluminescent Tunicates. In *Endocytobiology, Endosymbiosis and Cell Biology*, Vol. 1. W. Schwemmler and H. E. A. Schenk, eds., New York: Walter de Gruyter and Co., pp. 461-466.

Bacterial luciferase activity is demonstrated in extracts of the tunicate *Pyrosoma*. The kinetics are typical of symbiotic *Photobacterium* species. No *Photobacterium* can be cultured from bacteria isolated from waters surrounding the *Pyrosoma*. Previous investigations establishing the existence of inclusions of bacteria within *Pyrosoma* are reported. The conclusion is reached that luminescence in *Pyrosoma* is due to luminous bacterial symbionts, but the nature of the control mechanism that allows *Pyrosoma* to flash upon stimulation instead of glow constantly is not established.

482. Nealson, Kenneth H., Margo G. Haygood, Bradley M. Tebo, Mark Roman, Edward Miller and John E. McCosker (1984). Contribution by Symbiotically Luminous Fishes to the Occurrence and Bioluminescence of Luminous Bacteria in Sea Water. *Microb. Ecol.* 10:69-77.

Seawater samples from a variety of locations contained viable luminous bacteria, but luminescence was not detectable although the system used to measure light was sensitive enough to measure light from a single, fully induced luminous bacterial cell. When the symbiotically luminous fish *Cleidopus gloriamaris* was placed in a sterile aquarium, plate counts of water samples showed an increase in luminous colony-forming units. Luminescence also increased, decreasing when the fish was removed. Light measurements of water samples from a sterile aquarium containing *Photoblepharon palpebratus*, another symbiotically luminous fish, whose bacterial symbionts have not been cultured, showed a similar pattern of increasing light which rapidly decreased upon removal of the fish. These experiments suggest that symbiotically luminous fishes release brightly luminous bacteria from light organs into their environment and may be a source of planktonic luminous bacteria. Although planktonic luminous bacteria are generally not bright when found in seawater, water samples from environments with populations of symbiotically luminous fish may show detectable levels of light.

483. Nealson, Kenneth H. and Larry B. Stotts (1981). Foreword. In *Bioluminescence: Current Perspectives*. Kenneth H. Nealson, ed., Minneapolis, (Minnesota): Burgess Publishing Co., pp. 1-9.

Three areas of basic research in bioluminescence are discussed. These are: (1) new approaches and techniques for light measurement and methods for data handling; (2) spectral and kinetic characteristics of bioluminescence; and (3) the distribution and activity of luminous organisms in situ. A brief summary of current knowledge is provided. The concept of an optical communications system involving satellite laser transmitters is also described and questions concerning the effects of bioluminescence on that system are addressed.

484. Nealson, Kenneth H. and Jon A. Warner (1982). Mechanisms of Bioluminescence: Kinetic-Spectral and Biochemical Properties as a Probe of Marine

Communities and Interactions. Progress Report Abstracts, Office of Naval Research, December, pp. 35-37.

**ABSTRACT.** A station for continuous monitoring of bioluminescence down to 200 m has been deployed in Scripps Canyon. Luminescence activity has been monitored for ten months. Flash rates have been observed to increase early in the night, decrease through the middle, and increase to high levels near morning. Distinct flash types can be identified and suggest the possibility of identifying luminous organisms by their flash kinetics and spectra. Laboratory measurements confirm this possibility. A small molecule, [N-( $\beta$ -ketocaproyl) homoserine lactone] produced by luminous bacteria has been shown to control the level of light emission in bacteria in various oceanic environments. A yellow fluorescent protein has also been isolated, purified and characterized from yellow-emitting luminous bacteria. It has been shown that the ocean is continuously inoculated with bacteria from the luminous organs of fish and squid. The lux gene has been cloned.

485. Neary, A. P. and C. S. J. Walpole (1986). Bioluminescence-Chemical Light. *Sci. Prog.* (Oxford) 70:145-169.

The scale of the phenomenon of bioluminescence, and the progress made towards our understanding of it, is discussed. The mechanisms of chemiluminescence and bioluminescence reactions are described from the standpoint of the organic chemist, with particular reference to the best known examples. An account is given of the chemical models which have been successful in the investigation of bioluminescence. The evolution and possible function of the phenomenon are discussed.

486. Neering, Ian R. and Martin W. Fryer (1986). The Effect of Alcohols on Aequorin Luminescence. *Biochem. Biophys. Acta* 882:39-43.

The effect of alcohols from ethanol to octanol on aequorin luminescence was biphasic; enhancement of both peak light and total photon yield at low concentrations and inhibition of these parameters at high concentration. The potency of alcohols to exert these effects was in the same order as the oil/water partition coefficients of the alcohols. It is argued that neither of these effects is related to calcium binding by aequorin, since alcohols enhanced calcium-independent luminescence and the inhibition

of responses is not associated with a reduction in the rate of aequorin "consumption" on binding of calcium.

487. Nicol, J. A. C. (1978). Bioluminescence and Vision. In *Bioluminescence in Action*. Peter J. Herring, ed., New York: Academic Press, pp. 367-398.

The transmission of light through seawater is briefly and generally described. The spectral emission from various luminescent organisms is charted and compared to that of downwelling light. Recorded luminescence intensities from various organisms are reported. These physical characteristics of bioluminescence are matched to the visual capabilities of fish primarily, but cephalopods and shrimp are also mentioned. The distribution and function of luminescence in the ocean and location of photophores on the organisms are also discussed. Finally, the diel vertical migration of planktonic and nektonic organisms is related to ambient light levels.

488. Nicolas, Gisèle, Marie-Thérèse Nicolas, Jean-Marie Bassot and J. Woodland Hastings (1985). Cryofixation et Marquage Immunocytochimique à l'Or Colloïdal de la Luciferase chez les Dinoflagellés Bioluminescents. *Biol. Cell.* 53(3):23A (French).

**ABSTRACT.** Intracellular microsomes of bioluminescence in *Gonyaulax* that fluoresce under UV illumination have been observed using an image-intensified microscope. The presence of luciferase in these microsomes has been established by immunological reaction with antiluciferase antibody, immunogold fixation, and either chemical fixation or fast cryofixation with osmium compounds.

489. Nicolas, Marie-Thérèse, Jean-Marie Bassot and Osamu Shimomura (1981). Caractérisation d'une Photoprotéine Nouvelle dans le Système Bioluminescent des Annélides Polynolines. *C.R. Acad. Sci* (Paris) 293 (Ser. III):777-780. (French).

A membrane protein is extracted from the scale-worm system with Triton X-100 and isolated by chromatography. It emits at 510 nm upon addition of several reagents which produce superoxide or hydroxyl radicals, in presence of  $O_2$ . It is not triggered by  $Ca^{++}$  ions. It is a new photoprotein, named polynoidin. It is not fluorescent and is distinct from the fluorescent substance of the photosomes, identified as riboflavin. In vivo the oxidation of riboflavin could produce  $O_2$  radicals.

490. Nicolas, Marie-Thérèse, Carl H. Johnson, Jean-Marie Bassot and J. Woodland Hastings (1985). Immunogold Labeling of Organelles in the Bioluminescent Dinoflagellate *Gonyaulax polyedra* with Anti-Luciferase Antibody. *Cell Biol. Int. Rep'ts* 9(9):797-802.

A polyclonal antibody directed against the luciferase of the luminous dinoflagellate *Gonyaulax polyedra* labels both dense vesicles and trichocyst sheaths, as visualized in the electron microscope after treatment of antibody-reacted sections with an immunogold probe. Because of their similar size, shape, and localization, the dense vesicles seen with the electron microscope are postulated to correspond to autofluorescent particles seen with the fluorescent microscope, which are known to be the origin of bioluminescent flashes in this alga. The explanation for the trichocyst sheath-specific labeling is less evident. The possibility that a second antibody of different specificity is involved has not been excluded but seems unlikely. Alternatively, it could be due to a different but antigenically cross-reacting protein. But the possibility that luciferase itself occurs in two different organelles is intriguing and consistent with previous biochemical studies of cell extracts.

491. Nicolas, Marie-Thérèse, Gisèle Nicolas, Carl H. Johnson, Jean-Marie Bassot and J. Woodland Hastings (1985). Fast Freeze-Freeze Substitution and Immunogold Labeling of Bioluminescent Organelles in Dinoflagellates. *Amer. Soc. for Cell Biology 25th Ann. Meet.*

**ABSTRACT.** Trichocyst sheaths and spherical dense vesicles resembling peroxisomes are labeled by immunogold labeling. Fast freeze fixation and freeze substitution then allow examination of the ultrastructure. These techniques and other observations lead to the conclusion that the labeled vesicles are the principal bioluminescent organelles in *Gonyaulax polyedra*.

492. Nicolas, Marie-Thérèse, Gisèle Nicolas, Carl H. Johnson, Jean-Marie Bassot and J. Woodland Hastings (1987). Fast Freeze-Freeze Substitution and Immunogold Labeling of Bioluminescent Organelles in Dinoflagellates. In *Bioluminescence and Chemiluminescence: New Perspectives*, J. Schölmerich, R. Andreeson, A. Kapp, M. Ernst and W. G. Woods, eds., New York: John Wiley and Sons, pp. 413-414B.

Immunocytochemical staining with a polyclonal antiluciferase antibody combined with immunogold labeling after fast-freeze fixation and freeze substitution with acetone or acetone/osmium tetroxide labels two structures in *Gonyaulax polyedra*: (1) dense bodies which may be identified as the luminous organelles; and (2) the trichocyst sheaths. The ultrastructure of the organelles is examined and they are tentatively identified with scintillons. It is suggested that flashes are triggered in vivo by the voltage-gated entry of H<sup>+</sup> ions from the vacuole.

493. Nicolas, Marie-Thérèse, Gisèle Nicolas, Carl H. Johnson, Jean-Marie Bassot and J. Woodland Hastings (1987). Characterization of the Bioluminescent Organelles in *Gonyaulax polyedra* (Dinoflagellates) after Fast-freeze Fixation and Antiluciferase Immunogold Staining. *J. Cell Biol.* 105:723-735.

To characterize the microsources of bioluminescent activity in the dinoflagellate *Gonyaulax polyedra*, an immunogold labeling method for using a polyclonal antiluciferase was combined with fast-freeze fixation and freeze substitution. The quality of the preservation and the specificity of the labeling were greatly improved compared to earlier results with chemical fixation. Two organelles were specifically labeled: cytoplasmic dense bodies with a finely vermiculate texture, and the mature trichocysts, labeled in the space between the shaft and the membrane. The available evidence indicates that the dense bodies are the light-emitting microsources observed in vivo. The dense bodies appear to originate in the Golgi area as cytoplasmic densifications and, while migrating peripherally, come into contact with the vacuolar membrane. Mature organelles protrude and hang like drops in the vacuolar space, linked by narrow necks to the cytoplasm. These structural relationships, not previously apparent with glutaraldehyde fixation, suggest how bioluminescent flashes can be elicited by a proton influx from a triggering action potential propagated along the vacuolar membrane. Similar dense bodies were labeled in the active particulate biochemical fraction (the scintillons), where they were completely membrane bound, as expected if their necks were broken and resealed during extraction. The significance of the trichocyst reactivity remains enigmatic. Both organelles were labeled with affinity-purified antibody, which makes it unlikely that the trichocyst labeling is due to a second antibody of different specificity. But trichocysts are not

bioluminescent; the cross-reacting material could be luciferase present in this compartment for some other reason, or a different protein carrying similar antigenic epitopes.

494. Nicolas, Marie-Thérèse, Beatrice M. Sweeney and J. Woodland Hastings (1987). The Ultrastructural Localization of Luciferase in Three Bioluminescent Dinoflagellates, Two Species of *Pyrocystis*, and *Noctiluca*. Using Antiluciferase and Immunogold Labelling. *J. Cell Sci.* 87:189-196.

In order to discover the intracellular location of luciferase in dinoflagellates, sections from a number of species were treated with a polyclonal anti-luciferase and the bound antibody was visualized at the electron-microscope level by indirect immunogold labelling. In two species of *Pyrocystis* and in *Noctiluca*, as in *Gonyaulax*, antibody became bound to dense vesicles, which correspond in size and position to light-emitting bodies detected in previous work. These vesicles resemble microsomes, are bounded by a single membrane and sometimes project into the vacuole. Unexpectedly, the trichocysts of *Gonyaulax* and *Noctiluca* and the related mucocysts of *Pyrocystis* also bound the antibody. This cross-reaction seems quite independent of bioluminescence, since the trichocysts of the nonluminous *Cachonina* also reacted positively. The possibility is discussed that a protein, different from luciferase but having some antigenic similarity, is present in trichocysts and related organelles.

495. Njus, David, Van D. Gooch and J. Woodland Hastings (1981). Precision of the *Gonyaulax* Circadian Clock. *Cell Biophysics* 3:223-231.

Under constant conditions, the circadian bioluminescent glow rhythm in populations ( $10^5$  cells) of *Gonyaulax polyedra* is accurate to within 2 min/day. On successive days following the transfer to constant conditions, however, the glow exhibits a progressively broader waveform, implying that individual clocks in the population are drifting out of synchrony. Analysis of the glow waveform suggests that the standard deviation in circadian period among individual clocks is about 18 min and that the period of a given clock varies by less than this from one day to the next.

496. Njus, David and Elijah Swift (1979). Bioluminescence. In *Toxic Dinoflagellate Blooms*,

Dennis L. Taylor and Howard H. Seliger, eds., New York/North Holland: Elsevier, pp. 459-462.

The discussions of the workshop on bioluminescence during the Second International Conference on Toxic Dinoflagellate Blooms are reported. The topics discussed included the ecological importance of bioluminescence, the physiology of stimulation and inhibition, and new developments in biochemistry.

497. O'Brien, Catherine H. and Ronald K. Sizemore (1979). Distribution of the Luminous Bacterium *Beneckea harveyi* in a Semitropical Estuarine Environment. *Appl. Environ. Microbiol.* 38(5):928-933.

Bioluminescent bacteria were found in the water column, sediment, shrimp and gastrointestinal tract of marine fishes from the semitropical estuarine environment of the East Lagoon, Galveston Island, Tex. Populations in the water column decreased during cold weather while sedimentary populations persisted. The highest percentages of luminous organisms were isolated from the gastrointestinal tract of marine fishes, where they persisted during 5 days of starvation. The presence of chitin temporarily increased intestinal populations. All isolates were *Beneckea harveyi*, whose natural habitat appears to be the gut of fishes and whose free-living reservoir appears to be marine sediments.

498. O'Callaghan, J. P., R. Stanek and L. G. Hyman (1984). On Estimating the Photoelectron Yield and the Resultant Inefficiency of a Photomultiplier-Based Detector. *Nucl. Instrum. Methods Phys. Res.* 225:153-163.

Three methods are presented for estimating the photoelectron yield from a photomultiplier illuminated by an LED. They show that the three estimates are consistent. These estimates disagree by about 25% from the popular but incorrect assumption that the pulse height distribution is Poisson-like in the number of photoelectrons. Further, computations involving Gaussian spreading and/or Landau fluctuations are then performed. These computations should model the behavior of actual scintillator or Cherenkov counters. These computations enable us to estimate how often a counter will miss a count.

499. O'Kane, Dennis J., Virginia A. Karle and John Lee (1985). Purification of Lumazine Proteins from

*Photobacterium leiognathi* and *Photobacterium phosphoreum*: Bioluminescence Properties. *Biochemistry* 24:1461-1467.

Bright strains of the marine bioluminescent bacterium *Photobacterium leiognathi* produce a "lumazine protein" in amounts comparable to that previously found in *Photobacterium phosphoreum*. New protocols are developed for the purification to homogeneity of the proteins from both species in yields up to 60%. In dimmer strains the amounts of lumazine protein in extracts are less, and also there is an accompanying shift of the bioluminescence spectral maximum to longer wavelength, 492 nm. Both types of lumazine proteins have identical fluorescence spectra, with maxima at 475 nm, so it is suggested that, whereas lumazine protein is the major emitter in bright strains, there is a second emitter also present with a fluorescence maximum at longer wavelength. The two species of lumazine protein have the same 276 nm/visible absorbance ratio, 2.2, but differ in visible maxima: *P. phosphoreum*, 417 nm; *P. leiognathi*, 420 nm. For the latter the bound lumazine has  $\epsilon_{420} = 10100 \text{ M}^{-1} \text{ cm}^{-1}$ , practically the same as in free solution. The two lumazine proteins also differ quantitatively in their effect on the in vitro bioluminescence reaction, i.e., at blue shifting the bioluminescence spectrum or altering the kinetics. The *P. phosphoreum* lumazine protein is more effective with its homologous luciferase or with *P. leiognathi* luciferase than is the lumazine protein from *P. leiognathi*. These differences may have an electrostatic origin.

500. O'Kane, Dennis J. and John Lee (1986). Purification and Properties of Lumazine Proteins from *Photobacterium* Strains. In *Bioluminescence and Chemiluminescence Part B (Methods Enzymol.* 133:149-172). Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 149-172.

Bacterial luciferase emission maxima in vitro range from 487 to 500 nm with most around 495 nm. The in vitro and in vivo emission maxima of *Vibrio* species are usually similar but other emission characteristics may be quite different. *Photobacterium* species, however, exhibit in vivo substantially blue-shifted emission maxima, as low as 472 nm, due to the presence of a blue-fluorescent protein that absorbs and reemits the energy from the bioluminescence reaction. Such proteins have been

identified in six *Photobacterium* strains. Techniques for preparing two of these and their physicochemical, biological and spectral properties are described along with possible mechanisms for excitation.

501. O'Kane, Dennis J., Ian B. C. Matheson and John Lee (1985). Quantum Efficiencies and Kinetics of Lumazine Protein Stimulation of Bacterial Bioluminescence. *Photochem. Photobiol.* 41(Suppl.):42S.

**ABSTRACT.** Lumazine proteins from *Photobacterium* increase the quantum efficiency of bioluminescence by about a factor of three and shift the emission spectrum toward the blue. The kinetics of the reaction differ for each luciferase and spectral analysis indicates more than one emission process.

502. Olesiak, Walter, Anne Ungar, Carl H. Johnson and J. Woodland Hastings (1987). Are Protein Synthesis Inhibition and Phase Shifting of the Circadian Clock in *Gonyaulax* Correlated? *J. Biol. Rhythms* 2(2):121-138.

They describe a method whereby the effect of protein synthesis inhibitors upon protein synthesis in *Gonyaulax* cultures may be reliably measured. Using this method, they found that protein synthesis inhibition and clock resetting were correlated, but that the correlation was not as close as has been reported in other systems. The effect of the inhibitors anisomycin and cycloheximide upon phase shifting of the circadian clock was a function of the illumination and temperature conditions to which the cells were subjected, but these factors did not appear to influence the inhibition of protein synthesis by these drugs. Cellular protein synthesis did not recover immediately from the inhibitors' effects; depending upon the previous concentration of the inhibitor, translational recovery from the drugs may require hours. This observation has important implications for the analysis of any phase response curve when the stimulus is a chemical.

503. Oliver, James D., Robert A. Warner and David R. Cleland (1982). Distribution and Ecology of *Vibrio vulnificus* and Other Lactose-Fermenting Marine Vibrios in Coastal Waters of the Southeastern United States. *Appl. Environ. Microbiol.* 44(6):1404-1414.

Water, sediment, plankton and animal samples from five coastal sites from North Carolina to Georgia were sampled for their lactose-fermenting vibrio

populations. Over 20% of all vibrios tested were sucrose negative and o-nitrophenyl- $\beta$ -D-galactopyranoside (ONPG) positive, suggesting identification as the human pathogen *Vibrio vulnificus*. These vibrios were isolated from all sample sites and sources (water, sediment, plankton and animals). Correlations with several of 19 environmental parameters monitored at each site were found for total vibrios. The presence of ONPG-positive, sucrose-negative vibrios was correlated with hydrocarbon levels in the water and, in the case of plankton samples, with salinity. A total of 279 sucrose-negative, ONPG-positive isolates were subjected to numerical taxonomic analysis, which resulted in three major clusters. Cluster I corresponded to and included 11 reference strains of *V. vulnificus*. Cluster II contained the largest number (133) of isolates, of which the great majority were bioluminescent. Although having a resemblance to *V. harveyi*, the isolates were ONPG positive and many were H<sub>2</sub>S positive. Cluster III consisted of strains similar to the group F vibrios (*V. fluvialis*). Of all of the isolates, 55% were luminescent, of which over 20% were lethal when injected into mice. Problems involved in detecting lactose fermentation among marine vibrios and the potential pathogenicity of these organisms are discussed.

504. Oliver, James D., Robert A. Warner and David R. Cleland (1983). Distribution of *Vibrio vulnificus* and Other Lactose-Fermenting Vibrios in the Marine Environment. *Appl. Environ. Microbiol.* 45(3):985-998.

During the summer of 1981, 3,887 sucrose-negative vibrios were isolated from seawater, sediment, plankton and animal samples taken from 80 sites from Miami, Florida, to Portland, Maine. Of these, 4.2% were able to ferment lactose. The lactose-positive strains isolated from the various samples correlated positively with pH and turbidity of the water, vibrios in the sediment and oysters and total bacterial counts in oysters. Negative correlations were obtained for water salinity. Numerical taxonomy was performed on 95 of the lactose-fermenting environmental isolates and 23 reference strains. Five clusters resulted, with the major cluster containing 33 of the environmental isolates and all of the *Vibrio vulnificus* reference strains. The 33 isolates, which produced an acid reaction in lactose broth within

hours of initial inoculation, represented 20% of all lactose-fermenting vibrios studied. These isolates were nearly identical phenotypically to clinical strains of *V. vulnificus* studied by the Center for Disease Control, Atlanta, Georgia, and by our laboratory, and their identification was confirmed by DNA-DNA hybridization studies. *V. vulnificus* was isolated from all sample types and from Miami to Cape Cod, Massachusetts, and comparison of the environmental parameter of the eight subsites yielding this species with those of all 80 subsites revealed no significant differences. The majority of the isolates were obtained from animals, with clams providing most (84%) of these. On injection into mice, 82% of *V. vulnificus* isolates resulted in death. Members of the remaining four clusters contained strains which differed from *V. vulnificus* in such phenotypic traits as luminescence and in urease or H<sub>2</sub>S production. None of the other reference cultures, including nine other *Vibrio* species, were contained in the remaining clusters and these isolates could not be identified. Most of these were also lethal for mice. Phenotypic differences, potential pathogenicity and geographic distribution of the five clusters were examined. It is concluded that *V. vulnificus* is a ubiquitous organism, both geographically and in a variety of environmental sources, although it occurs in relatively low numbers. The public health significance of this organism and of the other unidentified lactose-fermenting *Vibrio* species is discussed.

505. Orndorff, S. A. and Rita R. Colwell (1980). Distribution and Identification of Luminous Bacteria from the Sargasso Sea. *Appl. Environ. Microbiol.* 39(5):983-987.

*Vibrio fischeri* and *Lucibacterium harveyi* constituted 75 of the 83 luminous bacteria isolated from Sargasso Sea surface waters. *Photobacterium leiognathi* and *Photobacterium phosphoreum* constituted the remainder of the isolates. Luminescent bacteria were recovered at concentrations of 1 to 63 cells per 100 mL from water samples collected at depths of 160 to 320 m. Two water samples collected at the thermocline yielded larger numbers of viable, aerobic heterotrophic and luminous bacteria. Luminescent bacteria were not recovered from surface microlayer samples. The species distribution of the luminous bacteria reflected previously recognized growth patterns; i.e., *L. harveyi* and *V. fischeri* were predominant in the upper, warm waters (only one

isolate of *P. phosphoreum* was obtained from surface tropical waters).

506. Orzech, James K. and Kenneth H. Nealson (1984). Bioluminescence of Marine Snow: Its Effect on the Optical Properties of the Sea. In *Ocean Optics VII* (SPIE Vol. 489). Marvin A. Blizard, ed., Society of Photo-Optical Instrumentation Engineers, Bellingham, WA, pp. 100-106.

During two 60-m saturation dives, U. S. Navy divers hand-collected samples of marine snow (aggregates) and of surrounding water and made video recordings of aggregates passing through a loop used to determine their sizes and numbers. Analyses of the video recordings revealed that aggregates were abundant during both dives, accounting for 748 and 759 mL per cubic meter of seawater volume respectively. Although the total volume of aggregate material was similar, it was distributed quite differently between the two dives in 220 larger (mean volume 3.40 mL) and 595 smaller (mean volume 1.28 mL) aggregates per cubic meter. Laboratory analyses revealed that many of the aggregate samples were luminous, emitting light from two to six orders-of-magnitude greater than that produced in comparable volumes of surrounding water. We estimated the total light flux  $\phi(\lambda)$  per cubic meter of seawater ( $1.1 \times 10^9$  and  $3.2 \times 10^8$  quanta per second), as well as the portion of that flux which was due to the aggregates. For the two dives, 63 and 20 percent of the aggregate samples were luminous accounting for 97 and 44 percent of the total light flux  $\phi(\lambda)$ . These results indicate that marine snow is a variable source for light-scattering material and bioluminescence in the sea.

507. Orzech, James K. and Kenneth H. Nealson (1985). Marine Snow as an Emitter of Light in the Sea. *EOS* 66(51):1321.

**ABSTRACT.** Marine snow macroaggregates and surrounding water were hand-collected in separate syringes to a depth of 260 m by US Navy saturation divers. About half of the samples emitted light from two to six orders of magnitude greater than that produced in an equal volume of surrounding water. Major producers were bacteria, dinoflagellates and radiolarians associated with the marine snow.

508. Pérès, Jean-Marie, Pierre Laborde, Jean-Claude Romano and Yolanda de Souza-Lima (1986). Eau

Rouge à *Noctiluca* sur la Côte de Provence en Juin 1984 Essai d'Interpretation Dynamique. *Ann. Inst. Oceanogr.* (Paris) 62(1):85-116. (French).

A theory to account for a red tide of *Noctiluca scintillans* that occurred near the mouth of the Rhine River in June 1984 (and, extended, to red tides in general) is proposed. The river discharges huge amounts of nutrients into the sea, after which the water column achieves relative stability. Changes in physical factors induce a bloom of diatoms and *Prorocentrum*. The population of *Noctiluca* in deep, distant neritic waters begins to increase. Swarms form and begin to move toward the surface and shoreline. When the swarms reach a density of several dozens to 1000 cells per liter, they may integrate into a well-balanced ecosystem with an important trophic system, or they may overwhelm an ecosystem with a low biomass, forming a red tide. This population explosion is quickly followed by mass extinction, from which only a few individuals escape.

509. Petushkov, V. N., G. A. Kratasyuk, V. A. Kratasyuk and P. I. Belobrov (1982). Thermal Inactivation of Bacterial Luciferase. *Biochemistry (USSR)* 47(11):1773-1777 (Russian) :1504-1508 (English).

The kinetics of the thermal inactivation of bacterial luciferase was studied. The substrates of the enzyme provide a weak protective effect from inactivation. EDTA, dithiothreitol, and bovine serum albumin substantially stabilize luciferase. The proposed mechanism of inactivation of the enzyme includes oxidation of SH groups and dissociation of the dimer into inactive monomers.

510. Petushkov, V. N., G. A. Kratasyuk, N. S. Rodionova, A. M. Fish and P. I. Belobrov (1984). Two-Enzyme NADH:FMN-Oxidoreductase-Luciferase System from Luminescent Bacteria. *Biochemistry (USSR)* 49(4) :692-702 (Russian) :593-603 (English).

The two-enzyme system NADH:FMN-oxidoreductase-luciferase system from the luminescent bacteria *Beneckea harveyi* and *Photobacterium leiognathi* was studied. Enzymes with high specific activity were obtained by means of gel filtration through Biogel P-100 and chromatography on hydroxyapatite. The main kinetic characteristics of the enzyme preparations and the pH- and temperature-dependences of the activity of the two-enzyme system were determined. A mathematical model of the

functioning of this system was constructed on the basis of the experimental data. The model takes into account the non-enzymatic oxidation of FMNM<sub>2</sub> by oxygen, the inhibition of luciferase by FMN, and the presence of a long-lived intermediate luciferase in the system. Analytical equations for the dependence of the bioluminescence intensity of the two-enzyme luciferase-reductase system on time and on the concentration of the enzymes and their substrates were determined for specific cases. It was found that coupling between the reductase and luciferase is realized through the free intermediate product FMNH<sub>2</sub>. The enzymatic preparations obtained were used for a determination of microquantities of NADH with a sensitivity of 10–15 mole.

511. Petushkov, V. N., N. S. Rodionova and P. I. Belobrov (1985). Efficiency of the Functioning of the Bienzymatic System NADH:FMN Oxidoreductase-Luciferase of Luminescent Bacteria. *Biochemistry* (USSR)50(3):401–405 (Russian):338–342 (English).

The bienzymatic system NADH:FMN oxidoreductase-luciferase of luminescent bacteria is discussed as a transformer of reducing equivalents of NADH molecules into light quanta. The efficiency of the work of this transformer, determined according to the number of the quanta emitted calculated per NADH molecule, was  $1.1 \times 10^{-3}$  at a luciferase concentration of 14 µg/mL. It was shown that the efficiency does not depend on the NADH concentration and the amount of reductase in the reaction mixture. The optimum concentrations of FMN ( $10^{-7}$ M) and bovine serum albumin ( $1.4 \times 10^{-6}$  µM) at which the efficiency of the transformer is a maximum were found.

512. Popova, L. Yu. and A. N. Shenderov (1983). Pathway of Synthesis of Aldehyde Factor—the Main Substrate of Luciferase. *Biochemistry* (USSR)48(6):983–990 (Russian):843–849 (English).

The stimulation of the level of luminescence and the level of the cellular aldehyde factor was studied during the growth of one aldehyde-dependent mutant on a medium conditioned by other aldehyde-dependent mutants. It was found that the aldehyde factor is synthesized in five successive steps and, accordingly, five precursors and five enzymes are involved in its synthesis. The metabolite accumulated in the conditioned medium increases both the level of

the cellular aldehyde factor and that of luciferase. It is assumed that some precursors of the synthesis of the aldehyde factor are involved in the regulation of the development of luminescence.

513. Popova, L. Yu., A. N. Shenderov, and N. I. Luts kaya (1982). The Structural Organization of the Luminescent System of *Photobacterium leiognathi*. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, Krasnoyarsk: eds., Akad. Nauk USSR, pp. 237–250.

A total of 150 mutants of *Photobacterium leiognathi* were categorized into seven independent mutant groups by cluster analysis. Analysis of the luminescence stimulating relationships among the groups suggested at least seven low-molecular-weight components involved in the light-emitting system. These include the aldehyde factor, synthesized in five stages, the autoinducer, synthesized in two stages, and all precursors. A mechanism also exists to coordinate synthesis of the aldehyde factor and autoinducer. In addition to these nine components, the complete luminescent system includes the two subunits of luciferase, a blue fluorescent protein, a repressor, and a factor responsible for glucose repression, for a total of 14 components in all.

514. Porter, Karen G. and James W. Porter (1979). Bioluminescence in Marine Plankton: A Coevolved Antipredation System. *Amer. Nat.* 114(3):458–460.

Theories on the origin of bioluminescence and its current functions in a variety of organisms are mentioned. The hypothesis that luminescence plays a role as part of a coevolved antipredation system is put forth. Supporting evidence with regard to selective feeding of copepods on nonluminous dinoflagellates in mixed populations, behavior of luminous copepods in the presence of predators and in response to mechanical stimulation, and pigmentation of the digestive tracts of transparent midwater and deep-sea planktivores is presented. It is suggested that this role for bioluminescence may be in addition to other functions.

515. Potts, G. W., J. W. Wood and J. M. Edwards (1987). Scuba Diver-Operated Low-Light-Level Video System for Use in Underwater Research and Survey. *J. Mar. Biol. Assoc. UK* 67:299:306.

A low-light-level (SIT) camera has been coupled to a portable JVC Video Cassette Recorder

(No. BR-6200E) contained in a waterproof Perspex case. Both camera and the VCR are operated by rechargeable batteries which give an operational performance of just over 3 h. The video signal is transmitted from the video camera to the VCR by means of a fiber optic link which offers advantages over conventional electrical connections. The system can be operated by a single scuba diver without the need for cables to an attendant boat. This enables the system to be used in areas not usually available to conventional underwater television systems and, with its low-light capability, makes the system particularly valuable in underwater behavioural observations where bright light may disturb light-sensitive organisms.

516. Prendergast, Franklyn G. (1980). Spectral Properties of Aequorin and the Green Fluorescent Protein of *Aequorea forskalea*. *Abstr., Amer. Soc. Photobiology, 8th Ann. Meet.*, p. 48.

**ABSTRACT.** Aequorin reacted with  $\text{Ca}^{++}$  produces a fluorescence emission spectrum identical to its bioluminescence emission spectrum. The fluorescence comes from a chromophore rigidly bound to the protein in the presence of  $\text{Ca}^{++}$ , but readily dissociable in its absence. The green-fluorescent protein, with a molecular weight of 30,000, contains a chromophore apparently identical to that of a green fluorescent protein from *Renilla*. These chromophores are also rigidly bound.

517. Primakova, G. A. (1984). Distribution of Luminescent Bacteria. In *Luminescent Bacteria* (English translation of *Svetyashchiyesya Bakterii*, Ye. N. Kondrat'yeva, ed., Moscow: Izdatel'stvo "Nauka,"), JPRS-UBB-85-018-L, 31 October 1985, pp. 23-30.

This chapter discusses the habitats and geographic distribution of free-living luminous marine bacteria. Vertical stratification is also discussed, with two layers identified, one from 200 m to 300 m, the other from 500 m to 700 m. A correlation between the upper layer and environmental factors optimum for bacterial growth is stated.

518. Primakova, G. A. (1984). Systematics of Luminescent Bacteria. In *Luminescent Bacteria* (English translation of *Svetyashchiyesya Bakterii*, Ye. N. Kondrat'yeva, ed., Izdatel'stvo "Nauka," Moscow). JPRS-UBB-85-018-L, 31 October 1985, pp. 5-22.

This book chapter discusses various taxonomic classification systems for luminous bacteria, including

the most recent widely accepted one, which places all marine luminous bacteria in two genera, *Vibrio* and *Photobacterium*. It presents a diagnostic scheme for rapid identification of luminous bacterial species and discusses their phylogeny and extinction kinetics.

519. Primakova, G. A., T. P. Turova, T. I. Vorob'yeva, A. M. Fish and A. S. Antonov (1983). Determination of the Taxonomic Status of Psychrophilic Luminescent Bacterial Cultures by Molecular DNA-DNA Hybridization. *Microbiology (USSR)* 52(2) :290-293 (Russian) :233-237 (English).

In vitro DNA-DNA hybridization was used to determine the extent of affinity between the DNA sequences of unidentified psychrophilic strains with the DNA of luminescent bacteria of genera *Photobacterium* and *Beneckea*. It was found that DNA of the strains investigated has maximum similarity with the DNA of *Photobacterium phosphoreum* (56-78% homology). The results of hybridization between the DNA of psychrophilic strains and *P. phosphoreum* and *P. leiognathi* DNA indicated that the extent of affinity between the genomes is characteristic for different species of a single genus.

520. Primakova, G. A., T. I. Vorob'yeva and A. M. Fish (1982). Taxonomic Position of Psychrophile Strains Group in the Luminous Bacteria System. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 227-236.

A strain of luminous bacteria which grows at temperatures approaching 0°C, with a growth optimum of 14-16°C and a luminescence optimum of 20-22°C, is reported isolated from waters of the subarctic Pacific region. It is tentatively identified as belonging to the genus *Phosphoreum*. It is characterized by "rapid" kinetics.

521. Primakova, G. A., T. I. Vorob'yeva, S. E. Medvedeva and A. M. Fish (1981). Morphology and Ultrastructure of Psychrophilic Luminous Bacteria. *Microbiology (USSR)* 50(3) :487-492 (Russian) :344-349 (English).

The morphology and ultrastructure of psychrophilic luminous bacteria, isolated from water from the subarctic zone of the Pacific Ocean, were studied. Cells of the recently isolated luminous bacteria are gram-variable and pleomorphic, undergo morphological changes during growth, and divide by

fission or budding. Study of the ultrastructure of psychrophilic luminous bacteria revealed features also typical for mesophilic photobacteria: location of the nucleoid, presence of poly- $\beta$ -hydroxybutyrate, and formation of internal membrane structures and vesicular projections from the outer cell-wall membrane. A particular characteristic of psychrophilic luminous bacteria is variation in the thickness of the cell wall resulting from the formation of a microcapsule and polysaccharide-type slime.

522. Ramamoorthi, K. and N. Jayabalan (1982). Free-living and Symbiotic Bioluminescent Bacteria. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 279-290.

Luminous bacteria are isolated from four different biotypes—marine, estuarine, backwater, and mangrove—and luminous fishes belonging to three genera of the family Leiognathidae—*Secutor*, *Gazza*, and *Leiognathus*—near Porto-Novo, India. *Beneckea* strains predominate in the water in all four biotypes, while only *Photobacterium leiognathi* is found in the photophores of the fishes.

523. Ramesh, A. (1984). Role of Bioluminescence in Marine Fisheries. *Seafood Export J.* 16(5):1-3.

The use of bioluminescence of dinoflagellates by fishermen to locate fish schools is documented along the Pacific coast of North America, the Malay and Indian coasts of the Indian Ocean and in the Arabian Sea. Schools of self-luminous fish can also be located by their light emission. The use of fish light organs as bait is described. Airborne remote sensing of fish schools using low-light-level image-intensifying television camera systems is documented in numerous oceanic areas.

524. Ramesh, A. (1986). Ecophysiological Studies on Luminous Bacteria of Vellar Estuary. Ph.D. Dissertation, CAS in Marine Biology, Annamalai University, Portonovo, India.

This thesis charts the variations in bacterial concentrations in the water column and sediment of the Vellar estuary and on the skin and gill and in the gut of two nonluminous fish living there and relates these variations to seasonal changes in environmental parameters. Three species of luminous bacteria, *Vibrio harveyi*, *V. fischeri* and *Photobacterium leiognathi*, were found, with *V. harveyi* dominant. A seasonal

cycle in the water column and sediment, apparently governed by salinity, was observed. Optimal growth conditions were also studied.

525. Ramesh, A., B. Loganathan and V. K. Venugopalan (1985). Commensal Luminous Bacteria of the Coelenterate, *Pteroeides* sp. *Curr. Sci. (India)* 54(12):582-583.

The luminous bacterium *Vibrio harveyi*, only, was found commensally associated with the coelenterate *Pteroeides* in its coelomic fluid. *V. harveyi* survived even though *Pteroeides* lacks a well-defined gut and possesses an antimicrobial capability.

526. Ramesh, A., B. Loganathan and V. K. Venugopalan (1985). Enteric Luminous Bacteria of Bivalves from Portonovo Waters. *J. Singapore Nat. Acad. Sci.* 14:116-119.

Luminous bacteria associated with the gut of some marine bivalves, viz. *Meretrix meretrix*, *M. casta*, *Donax cuneatus*, *Katelysia opima* and *Crassostrea madrasensis* were studied in relation to their environment. Qualitative and quantitative investigations were carried out. Of the three regions of the gut maximum luminous procaryotes were found in the hind gut in most of the bivalves. The fecal matter in the hind gut served as an ideal inoculum for the proliferation of these microbes. *Vibrio harveyi* was the predominant species recorded from the gut, water and sediment whereas *V. fischeri* was recorded sporadically from the gut and water only. The nutritional versatility of *V. harveyi* may probably account for its cosmopolitan distribution. From the results of the present study, it could be inferred that a regular cycling of these microbes occurs between the enteric habitat and the surrounding milieu.

527. Ramesh, A., G. Balakrish Nair, Martin Abraham, R. Natarajan and V. K. Venugopalan (1987). Seasonal Distribution of Luminous Bacteria in the Tropical Vellar Estuary. *Microbios* 52:151-159.

Spatiotemporal distribution of luminous microflora in water in relation to environmental parameters was studied at two stations located in the Vellar estuary. Luminous bacteria exhibited a marked seasonal cycle with very low counts during monsoon months followed by an increase in postmonsoon and peak counts during summer. Of all the environmental parameters monitored, salinity appeared to dictate the distribution of luminous procaryotes, as the

increase/decrease in the counts corresponded with fluctuations in salinity. Also higher counts of luminous microflora were discernible in the bottom waters than in the surface waters. Species composition of the isolates revealed dominance by *Vibrio harveyi*. *Vibrio fischeri* and *Photobacterium leiognathi* showed a limited distribution, being restricted to one station only, viz, the mouth of the estuary.

528. Ramesh, A., R. Nandakumar and V. K. Venugopalan (1986). Enteric Luminous Microflora of the Pond-Cultured Milk Fish *Chanos chanos* (Forsk.). *Microb. Ecol.* 12:231-235.

Qualitative and quantitative investigations were made on the luminous bacteria associated with the gut of pond-cultured milk fish *Chanos chanos*. Significant differences in luminous bacterial numbers were found between gut and pond water and between gut and pond sediment, but not between pond water and sediment. No significant variation in luminous bacterial population among the gut regions was observed. The quantity of ingesta in the fish gut does not appear to influence the biomass of luminous bacteria. *Vibrio harveyi* and *V. fischeri* were the two most commonly encountered species, and of the two luminous species, *V. harveyi* was predominant.

529. Ramesh, A. and V. K. Venugopalan (1983). Enteric Luminous Prokaryotes of Two Marine Gastropods of Portonovo Waters. *Abstr., 15th Pacific Science Cong.* 2:193.

**ABSTRACT.** The luminous bacterium *Vibrio harveyi* was found in the guts of the sea hare *Aplysia benedicti* and the whelk *Bullia tranquebarica* in much greater quantities than in the sediment and seawater in which they live. The midgut contained more bacteria than either the foregut or hindgut.

530. Ramesh, A. and V. K. Venugopalan (1986). Densities and Characteristics of Histamine-Forming Luminous Bacteria of Marine Fish. *Food Microbiol.* 3:103-105.

Of 30 luminous isolates of histamine-forming bacteria taken from the flesh of five species of fish from the local market, 18 were identified as *Vibrio harveyi*, seven as *V. fischeri* and five as *Photobacterium leiognathi*. These form about 30% of the total histamine-forming bacteria found.

531. Ramesh, A. and V. K. Venugopalan (1986). Ecophysiological Studies on Luminous Bacteria Associated with Marine Gastropods. *Second Int. Colloq. Marine Bacteriology*, pp. 445-450.

Information available on the association of luminous bacteria with marine invertebrates is limited. Hence, qualitative and quantitative investigations were undertaken with a view to understand the distribution of luminous microflora in relation to the environmental factors and also in the gut of two marine gastropods, *Aplysia benedicti* (Eliot) and *Bullia tranquebarica* (Roding) from Portonovo waters of the east coast of India. The gut of the gastropods harboured maximum number of luminous bacteria when compared to the water and sediment. Qualitative analysis revealed the presence of two luminous bacterial components, viz., *Vibrio harveyi* and *V. fischeri*. *V. fischeri* was not found in association with *A. benedicti*. The isolates of the luminous bacterial species were subjected to different physiological tests such as tolerance to sodium chloride, pH and temperature. Both the species grew well at 3-6% NaCl and at 7-8 pH. All the isolates registered good growth at 28°C, whereas isolates of *V. fischeri* were found to grow well at 15°C also. Both isolated strains exhibited chitinolytic activity.

532. Reif, Wulf-Ernst (1985). Functions of Scales and Photophores in Mesopelagic Luminescent Sharks. *Acta Zool. (Stockholm)* 66(2):111-118.

In sharks bioluminescence is only known from the family Squalidae. It evolved independently in two out of six squalid subfamilies, Dalatiinae and Etmopterinae. The distribution of photophores was mapped in several species. It is suggested that in the Dalatiinae, which do not school but migrate vertically, luminescence serves as ventral countershading. The Etmopterinae school and feed close to the bottom. Their luminescence is an aid in schooling. Four different placoid scale patterns are found in luminescent sharks and they allow accommodation of the photophores in the skin.

533. Rensing, Ludger, Walter Taylor, Jay C. Dunlap and J. Woodland Hastings (1980). The Effects of Protein Synthesis Inhibitors on the *Gonyaulax* Clock. II. The Effect of Cycloheximide on Ultrastructural Parameters. *J. Comp. Physiol.* B138:9-18.

Circadian changes in chloroplast shape and distribution within the cell are observed. Chloroplast portions penetrate toward the center of the cell from the periphery only during photophase. Intralamellar distances do not change during the course of a day. Circadian rhythms are detected in the percentage of two and three-stacked thylakoid lamellae and the number of starch granules present in defined regions of the cell. One  $\mu\text{M}$  cycloheximide does not immediately affect the ultrastructural parameters measured but does shift the measured rhythms by 8–12 hours.

534. Reynolds, George T. (1980). Applications of Image Intensification to Low Level Fluorescence Studies of Living Cells. *Microsc. Acta* 83(1):55-62.

Microscopic observations of weak fluorescence from living cells can be achieved by using image intensification techniques in situations where conventional film recording is not feasible. A brief description is given of experimental arrangements that have been used, involving recording the intensifier output alternately on film, or television vidicons. References are given to more detailed descriptions of particular systems, and an example is presented of the detection of  $\text{Ca}^{++}$  in *Haemaphysalis* by means of the fluorescence of chlorotetracycline.

535. Reynolds, George T. (1981). Instrumentation for the Detection of the Spectral Characteristics of Bioluminescent Organisms. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis, Minnesota: Burgess Publishing Co., pp. 29-40.

A spectroscopy image-intensifier system for observing weak bioluminescent spectra is described. Design considerations, calibration techniques and standards, schematics, correction curves, and output examples are provided. Its application to the measurement of bioluminescent spectra is discussed.

536. Reynolds, George T. (1981). Image Intensification in the Study of Bioluminescence. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis, Minnesota: Burgess Publishing Co., pp. 41-51.

The characteristics of image intensifiers are discussed. Cathode efficiency and uniformity, dark current, gain, and image quality are stressed as the most important parameters to consider. Film and

vidicons (plumbicons, SIVs and SITs) are discussed as recording devices. CCDs and CIDs, especially when coupled to high-gain microchannel plates, are mentioned as possible alternatives. Examples of applications to bioluminescence are shown.

537. Reynolds, George T., D. M. Nosenchuck, Alan J. Walton and Donald M. Anderson (1985). Response of Bioluminescent Dinoflagellates to Mechanical Stimulation. *Photochem. Photobiol.* 41(Suppl.):42S.

**ABSTRACT.** Image intensification studies of the response of bioluminescent dinoflagellates to changes in pressure, velocity (laminar and turbulent flow), acceleration and shear have been made. The response depends on the rates of change of these parameters and does not occur in regions of constant value.

538. Reynolds, George T. and D. L. Taylor (1980). Image Intensification Applied to Light Microscopy. *BioScience* 30(9):586-592.

The concept of image intensification applied to low-light biological problems, including bioluminescence, is discussed, and an experimental instrumental arrangement to view and record bioluminescence is shown. Spatial and temporal resolution and noise limitations are mentioned. Laboratory and field applications are given. Present and future instrumentation is considered.

539. Reynolds, George T. and Alan J. Walton (1983). Mechanical Stimulation of Bioluminescence in Dilute Suspensions of Dinoflagellates. *Biol. Bull.* 165:522.

**ABSTRACT.** Dilute suspensions of dinoflagellates (*Gonyaulax polyedra* and *Pyrocystis lunula*) (ca. 1000 cells/mL) are stimulated by a falling cone with an attached cylinder behind and the resulting patterns of bioluminescence recorded using image intensification. Luminescence is observed at the top and sides of the cone and side and trailing edge of the cylinder.

540. Reynolds, George T., Alan J. Walton and Donald M. Anderson (1984). Stimulation of Bioluminescence in Fluid Flow. *Biol. Bull.* 167:540.

**ABSTRACT.** Bioluminescence in *Gonyaulax polyedra* is stimulated by flow through capillaries, falling spheres and ellipsoids and rotating bodies of various shapes. Images videotaped through an image intensifier show that *G. polyedra* does not respond to

constant shear fields, overpressures, reduced pressures, velocities, or accelerations, but to variations in these parameters, as well as surface effects and bubble formation.

541. Rich, Edwin S. and John E. Wampler (1981). A Flexible, Computer-Controlled Video Microscope Capable of Quantitative Spatial, Temporal, and Spectral Measurements. *Clin. Chem.* 27(9):1558-1568.

A video microscope system has been constructed and tested that incorporates computer-controlled video cameras for high-resolution and low-light microscopy. The low-light camera system involves a dual microchannel plate-image intensifier capable of photon gain as high as 500,000 and a gated silicon-intensified target vidicon to achieve usable photon sensitivity with a noise equivalent signal of only 2 photons (500 nm) per pixel per second. We have compared the limitations and capabilities of this camera system with those of a high-resolution video camera and conventional photomicroscopy. Uses of the low-light camera coupled to a computer system include image acquisition of weak-light images from self-luminous specimens, fluorescence microscopy with weak exciting light, kinetic resolution of calcium-mediated events as monitored by the calcium-sensitive bioluminescence of aequorin, and spatially resolved spectroscopic measurements. Flexible use of this system in these various applications is possible because it allows operation with illumination intensities over a dynamic range of 100,000:1.

542. Rich, Edwin S. and John E. Wampler (1982). A Portable Photometer for Bioluminescence and Chemiluminescence Analysis. *Chem. Biomed. Environ. Instrumentation* 12(1):65-74.

A small, self-powered, portable photometer designed for field use is described. It has a four position sample holder, a digital peak hold, and integrator, autoranging over four decades and uses an LCD calculator as a readout device.

543. Ridgway, E. B. and A. E. Snow (1983). Effects of EGTA on Aequorin Luminescence. *Biophys. J.* 41 (2 pt.2):244a.

**ABSTRACT.** EGTA inhibits aequorin luminescence through two mechanisms: 1) its calcium chelating property; and 2) direct inhibition presumably by binding. EDTA has similar effects.

544. Riendeau, Denis and Edward A. Meighen (1979). Evidence for a Fatty Acid Reductase Catalyzing the Synthesis of Aldehydes for the Bacterial Bioluminescent Reaction: Resolution from Luciferase and Dependence on Fatty Acids. *J. Biol. Chem.* 254:7488-7490.

The enzyme responsible for the stimulation by ATP and NADPH of light emission catalyzed by bacterial luciferase has been partially purified from extracts of the luminescent bacterium, *Photobacterium phosphoreum*. The stimulatory activity was found to be stabilized by high concentrations of mercaptoethanol, permitting it to be separated from luciferase into an active and stable form and enabling further characterization of its functional properties. The activity of the enzyme was shown to be dependent not only on ATP and NADPH but also on the presence of a long-chain fatty acid, and was inhibited by the addition of NADH and horse-liver alcohol dehydrogenase. The specificity for fatty acids, as measured by the stimulation of luciferase activity, had a very limited range, with maximal luminescence being obtained with myristic acid and lower responses being observed only with tridecanoic and pentadecanoic acid. These results provide direct evidence in vitro for an enzyme in bioluminescent bacteria that functions as a fatty-acid reductase converting fatty acids to aldehydes which in turn can be utilized by luciferase in the light-emitting reaction.

545. Riendeau, Denis and Edward A. Meighen (1980). Co-induction of Fatty Acid Reductase and Luciferase during Development of Bacterial Bioluminescence. *J. Biol. Chem.* 255(24):12,060-12,065.

The luminescent bacterium *Photobacterium phosphoreum* has been shown to possess a fatty-acid reductase based on the stimulation of the aldehyde-dependent luminescent reaction on incubation of the enzyme with ATP, NADPH, and tetradecanoic acid. A direct, luciferase-independent assay for the fatty-acid reductase has now been developed using [<sup>3</sup>H]tetradecanoic acid as substrate and thin-layer chromatography to separate and identify the products of the reaction. Tritiated aldehyde was the only product of the reaction at early times of assay, and the amount produced was linearly dependent on time and extract concentration. The labeled aldehyde was further reduced to alcohol after prolonged incubation, indicating that long-chain aldehyde reductase(s) are

also present in bioluminescent bacteria. Measurement of the fatty-acid reductase activity in extracts during growth and development of the bioluminescent bacteria showed that the fatty-acid reductase activity is co-induced with luciferase, suggesting that these enzymes are coordinately regulated and directly implicating the fatty-acid reductase in aldehyde biosynthesis in the bacterial bioluminescent system.

546. Riendeau, Denis and Edward A. Meighen (1981). Fatty Acid Reductase in Bioluminescent Bacteria. Resolution from Aldehyde Reductases and Characterization of the Aldehyde Product. *Can. J. Biochem.* 59(6):440-446.

Fatty-acid reductase from the bioluminescent bacterium *Photobacterium phosphoreum* has been partially purified free of aldehyde reductase activity and with a low endogenous fatty acid content permitting the characterization of the aldehyde product of the reaction. Two aldehyde reductases, both dependent on NADH, were separated by anion-exchange chromatography from the fatty-acid reductase activity. The partially purified fatty-acid reductase catalyzed the synthesis exclusively of long-chain aldehydes from fatty acids in the presence of ATP and NADPH as demonstrated by the conversion of [ $^3\text{H}$ ]tetradecanoic acid to [ $^3\text{H}$ ]aldehyde. Comparison of the amount of [ $^3\text{H}$ ]aldehyde produced with the bioluminescence responses of luciferase to the aldehyde product and standard aldehydes, both with respect to maximum light intensity and luminescent decay, established that tetradecanoic acid had been converted to tetradecanal, the aldehyde of the same chain length. These results are consistent with a mechanism involving activation of the fatty acid with ATP followed by reduction of a fatty acyl intermediate to the corresponding aldehyde.

547. Riendeau, Denis, Angel Rodriguez and Edward A. Meighen (1982). Resolution of the Fatty Acid Reductase from *Photobacterium phosphoreum* into Acyl Protein Synthetase and Acyl-CoA Reductase Activities. Evidence for an Enzyme Complex. *J. Biol. Chem.* 257(12):6908-6915.

The biosynthesis of long chain aliphatic aldehydes for light emission in luminescent bacteria is catalyzed by a fatty-acid reductase in a reaction dependent on ATP and NADPH. Evidence has now been obtained which demonstrates that this reaction consists of two distinct steps: (1) activation of fatty

acid and (2) reduction of a fatty acyl intermediate to aldehyde. Fatty-acid reductase catalyzed the ATP-dependent incorporation of [ $^3\text{H}$ ]tetradecanoic acid into material insoluble in chloroform/methanol/acetic acid (3:6:1) (designated as acyl-protein synthetase activity) as well as the reduction of tetradecanoyl-CoA to fatty aldehyde in a reaction dependent on NADPH (acyl-CoA reductase activity). Both activities comigrated with the fatty-acid reductase on anion-exchange chromatography and gel filtration. Dye-ligand chromatography on Cibacron blue-Sepharose, however, resolved the fatty-acid reductase into its two functional components with the acyl protein synthetase activity being selectively adsorbed on this gel and eluted by a high concentration of sodium thiocyanate. Fatty-acid reductase activity could only be restored by mixing the two enzyme components. Both the molecular weight and the kinetic properties of the acyl protein synthetase were altered after resolution from the acyl-CoA reductase. The acyl protein product could be converted into a form soluble in organic solvents by treatment with hydroxylamine and eluted on gel filtration at the position of the synthetase indicating that it represented a covalent acyl protein intermediate of the enzyme. Analysis of the nucleotide products after incubation of the enzyme with [ $\alpha\text{-}^{32}\text{P}$ ]ATP and fatty acid showed that ATP was cleaved to AMP during fatty acid activation. These results provide evidence that the fatty-acid reductase is an enzyme complex containing at least two functional components, a synthetase involved in activation of the fatty acid to a fatty acyl intermediate with cleavage of ATP to AMP and a reductase that reduces the activated intermediate to aldehyde in an NADPH-dependent step.

548. Robison, Bruce H. (1985). Behavior Patterns of Mesopelagic Fishes. *EOS* 66(51):1264.

**ABSTRACT.** Mesopelagic fishes exhibit a complex variety of behavior patterns including 1) mimicry as a predator-avoidance strategy; 2) commensalism with siphonophores to gain food and protection against predators; 3) daily ambit dimensions; 4) feeding strategies; 5) spatial orientation; and 6) response to light and disturbances. These patterns emphasize stealth and concealment and are of obvious survival value in a habitat resembling a "bioluminescent minefield."

549. Robison, Bruce H. and Richard E. Young (1981). Bioluminescence in Pelagic Octopods. *Pacific Sci.* 35(1):39-44.

A peculiar circumoral organ in a pelagic bolitaenid octopus luminesced brilliantly when treated with  $H_2O_2$ . This is the first confirmed luminescent organ in an octopus. Similar organs are found only in females of *Eledonella pygmaea*, *Japetella diaphana* (sensu lato) approaching sexual maturity. The luminescent organs may function to attract mates.

550. Rodicheva, E. K. (1984). Growth and Luminescence of Luminous Bacteria. In *Luminescent Bacteria* (English translation of *Sveryashchiyesya Bakterii*, Ye. N. Kondrat'yeva, ed., Moscow: Izdatel'stvo "Nauka"), JPRS-UBB- 85-018-L, 31 October 1985, pp. 98-155.

The chemical composition, nutritional requirements, and metabolism of various species of luminous bacteria are presented and compared. Formula for optimal growth media are tabulated. The role of oxygen in cell metabolism and bioluminescence is discussed along with the effect of physical factors such as temperature and pressure on growth rates. Autoinduction and latency of light emission in new and log-phase cultures of luminous bacteria are described. Methods of continuous cultivation are given. Finally, a rhythmic oscillation in light output is identified and a model for this discovery is proposed.

551. Rodriguez, Angel and Edward A. Meighen (1985). Fatty Acyl-AMP as an Intermediate in Fatty Acid R- Aldehyde in Luminescent Bacteria. *J. Biol. Chem.* 260(2):771-774.

The acyl-protein synthetase component (50 K) of the fatty-acid reductase complex from the luminescent system of *Photobacterium phosphoreum* has been found to catalyze the activation of fatty acid via formation of an enzyme bound acyl-AMP (carboxyphosphate mixed anhydride) immediately prior to the acylation of the enzyme.  $PP_i$ -ATP exchange and nucleotide binding experiments are dependent on fatty acid and indicate that the fatty acyl-AMP is directly formed and that an adenylated enzyme intermediate is not part of the mechanism. The formation of acyl-AMP from fatty acid and ATP is reversible with a standard free energy of -2 kcal/mol, and is dependent on  $Mg^{2+}$ . The fatty acyl-AMP intermediate has been isolated and shown

to be part of the pathway of fatty-acid reduction. The 34 K component of the complex, which strongly stimulates the acylation of the 50 K protein by fatty acyl-AMP or fatty acid and ATP, is not required for the formation of acyl-AMP showing that it differentially affects the fatty acid activation and acylation steps catalyzed by the 50 K protein.

552. Rodriguez, Angel, Ivan R. Nabi and Edward A. Meighen (1985). ATP Turnover by the Fatty Acid Reductase Complex of *Photobacterium phosphoreum*. *Can. J. Biochem. Cell Biol.* 63:1106-1111.

A sensitive reverse-phase high-pressure liquid chromatographic assay for formation of AMP coupled with analysis of aldehyde production has been used to characterize the properties of the fatty-acid reductase complex of *Photobacterium phosphoreum*. The enzyme complex, which consists of three different polypeptides (34000, 50000, and 58000), has a high affinity for ATP ( $K_m = 20$  nM) and shows highest specificity with  $C_{14}$  fatty acids. Activation of the fatty acid is efficiently coupled to the reduction step showing a stoichiometry of one molecule of fatty acid reduced to aldehyde and one molecule of NADPH oxidized for every molecule of ATP converted to AMP. Reconstituted fatty-acid reductase (50000 and 58000) shows an ATP hydrolase activity that is independent of NADPH with the maximum amount of AMP formed limited by the amount of fatty acid in the assay, consistent with acyl-protein turnover experiments and the channelling of fatty acids to form acyl thioesters (-NADPH) or aldehydes (+NADPH). Addition of the 34000 polypeptide to the reconstituted enzyme results in stimulation of AMP formation (-NADPH) to a level far exceeding the amount of fatty acid, showing that the fatty acid can be recycled by the 34000 protein through its thioesterase activity. Also the 34000 protein is responsible for a two- to three-fold stimulation in the rate of ATP hydrolysis, suggesting that it can be involved in the stabilization of the enzyme complex.

553. Rodriguez, Angel, Denis Riendeau, and Edward A. Meighen (1983). Purification of the Acyl Coenzyme A Reductase Component from a Complex Responsible for the Reduction of Fatty Acids in Bioluminescent Bacteria. Properties and Acyltransferase Activity. *J. Biol. Chem.* 258(8):5233-5237.

The acyl-CoA reductase component of the fatty-acid reductase complex responsible for synthesis of long chain aldehydes for the bioluminescent reaction in bacteria has been purified to homogeneity. The enzyme copurified as part of the complex through the initial steps and was then resolved and further purified to give a single band on sodium dodecyl sulfate-gel electrophoresis of molecular weight 58,000. The molecular weight of the native enzyme was  $2 \times 10^5$ , indicating it was an oligomeric enzyme containing identical subunits. The acyl-CoA reductase had a high specificity for NADPH with a  $K_m$  value of 5  $\mu$ m at optimal concentrations of tetradecanoyl-CoA (5-10  $\mu$ m). The purified enzyme was discovered to have a high, intrinsic acyl-transferase activity forming thioesters with a number of different thiol compounds (mercaptoethanol, dithiothreitol, 2-mercaptoethyl ether). The rates of the acyl-transferase and acyl-CoA reductase reactions were similar to the rate of turnover of the fatty-acid reductase complex suggesting that fatty acid reduction and not activation controls the rate of conversion of fatty acids to aldehydes.

554. Rodriguez, Angel, Lee A. Wall, Luc M. Carey, Michael Boylan, David M. Byers and Edward A. Meighen (1984). Aldehyde Biosynthesis in Luminescent Bacteria. In *Analytical Applications of Bioluminescence and Chemiluminescence*, Larry J. Kricka, Philip E. Stanley, G. H. G. Thorpe and T. P. Whitehead, eds., New York: Academic Press, pp. 105-108.

In *Photobacterium phosphoreum* three polypeptides are involved in aldehyde biosynthesis: (1) an ATP-dependent acyl-protein synthetase; (2) an NADPH-dependent reductase; and (3) an acyl-CoA hydrolase to supply the fatty acids. In *Vibrio harveyi* only acyl-CoA reductase activity has been observed. A model for the system is presented.

555. Rodriguez, Angel, Lee A. Wall, Denis Riendeau and Edward A. Meighen (1983). Fatty Acid Acylation of Proteins in Bioluminescent Bacteria. *Biochemistry* 22:5604-5611.

Acylation of proteins with [ $^3$ H] tetradecanoic acid (+ATP) has been demonstrated in extracts of different strains of luminescent bacteria. The labeled polypeptides from *Photobacterium phosphoreum* (34 K and 50 K) have been identified as being involved in the acyl-protein synthetase activity that is part of a purified fatty-acid reductase complex

responsible for synthesis of long-chain aldehydes for the bioluminescent reaction. The two polypeptides (34 K and 50 K) have been separated from the acyl-CoA reductase enzyme (58 K) of the complex and resolved from each other, and the 50 K polypeptide was further purified to >95% homogeneity. Acylation of the 50 K polypeptide, alone, occurred at a low rate; however, the rate and level of acylation were greatly stimulated by the addition of either the 34 K or the 58 K polypeptide. Cold chase experiments demonstrated that the acylated 50 K polypeptide turned over in the presence of the 58 K polypeptide but not in a mixture containing only the 34 K and 50 K polypeptides. Furthermore, the acylated 50 K polypeptide could function as the immediate substrate for the fatty acyl-CoA reductase enzyme (58 K), being reduced with NADPH to aldehyde. The 34 K polypeptide was acylated only when all three polypeptides (34 K, 50 K, and 58 K) were present. Fatty acid reductase activity could be restored by mixing of only the 58 K (acyl-CoA reductase) and 50 K polypeptides, showing that the 50 K polypeptide is responsible for fatty-acid activation in the fatty-acid reductase complex and raising the question of what role the 34 K polypeptide plays in fatty-acid utilization in the luminescent system.

556. Rodriguez, Angel, Lee A. Wall, Denis Riendeau and Edward A. Meighen (1986). Fatty-acid reductase from *Photobacterium phosphoreum*. In *Bioluminescence and Chemiluminescence Part B (Methods Enzymol. 133:172-182)*, Marlene A. DeLuca and William McElroy, eds., New York: Academic Press pp. 172-182.

Fatty-acid reductase activity in *P. phosphoreum* can be divided into three components: (1) an acyl-protein synthetase; (2) a reductase; and (3) an acyltransferase which channels fatty acids into the reaction. ATP and NADPH are required. The mechanism of the reaction and chemical and physical characteristics of the reductase enzyme and the complex as a whole are described.

557. Roenneberg, Till and J. Woodland Hastings (1987). Influences on the Circadian Period in *Gonyaulax polyedra* by a tau-Shortening Substance and by Different Colors of Light. *Gordon Conf. on Chronobiology*.

**ABSTRACT.** Substances extracted from bovine brains or *Gonyaulax* but not bacteria shorten the

period of glow rhythm by up to 4.5 hours/day in cells kept in constant dim light. The activity is suppressed but not inactivated by red light and persists for more than a week after the cells have been washed with fresh medium. The effect is a function both of substrate concentration and cell density, which fact suggests uptake by the cells. In addition, blue light shortens and red light lengthens the period in an intensity-dependent fashion, whereas the period is independent of the intensity in white light. This fact suggests two photoreceptors affecting the circadian clock and that the extracted substance may be involved in a link between the clock and light reception.

558. Rosson, Reinhardt A. and Kenneth H. Nealson (1979). Control of Bacterial Bioluminescence. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 150.

**ABSTRACT.** Light may be emitted by luminous bacteria only when an autoinducer molecule excreted into the medium reaches a critical concentration. This concentration typically occurs at a specific cell density. Cells grown in dilute nutrient conditions sustain luminescence if the density is greater than the induction density, but luminescence per cell decreases sharply if cell densities are lowered.

559. Rosson, Reinhardt A. and Kenneth H. Nealson (1980). Chemostat Studies of Autoinduction of Bacterial Bioluminescence. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 80:170.

**ABSTRACT.** In a carbon-limited environment, the cell density of *Photobacterium fischeri*, *P. phosphoreum*, *P. leiognathi* and *Beneckea harveyi* decreased in proportion to reservoir carbon. Luminescence per cell in vivo and extractable luciferase per cell were constant when cultures were denser than the induction density, but dropped greatly below that density. *P. fischeri* luminescence was stimulated quickly in below-induction cell concentrations by addition of purified autoinducer. In one strain each of *P. phosphoreum* and *P. leiognathi* luminescence per cell in vivo was constant irrespective of cell density, an observation that suggests that the bioluminescence system in these strains is constitutive.

560. Rosson, Reinhardt A. and Kenneth H. Nealson (1981). Autoinduction of Bacterial Bioluminescence in a Carbon Limited Chemostat. *Arch. Microbiol.* 129:299-304.

Several strains of four species of luminous marine bacteria were maintained in a chemostat at a constant dilution rate and a variety of steady state densities by carbon (glycerol) limitation in order to study the relationship between culture density and bioluminescence activity. In general, luminescence per cell was constant at high culture density and decreased dramatically at low culture density. For *Vibrio fischeri*, luminescence decreased to nondetectable levels when the culture was maintained at low density; such dark cells were stimulated to synthesize luciferase and became luminous within minutes when purified autoinducer was added to the chemostat. Two strains, *Photobacterium phosphoreum* NZ11D and *Photobacterium leiognathi* S1, did not show the decrease in light intensity at low culture density that was characteristic of all other strains tested; they appeared to be constitutive for bioluminescence.

561. Ruby, Edward G., E. P. Greenberg and J. Woodland Hastings (1980). Planktonic Marine Luminous Bacteria: Species Distribution in the Water Column. *Appl. Environ. Microbiol.* 39(2):302-306.

Luminous bacteria were isolated from oceanic water samples taken throughout the upper 1000 m and ranged in density from 0.4 to 30 colony-forming units per 100 mL. Generally, two peaks in abundance were detected: one in the upper 100 m of the water column, which consisted primarily of *Beneckea* spp.; and a second between 250 and 1000 m, which consisted almost entirely of *Photobacterium phosphoreum*. The population of *P. phosphoreum* remained relatively stable in abundance at one station that was visited three times over a period of 6 months. However, the abundance of luminous *Beneckea* spp. isolated from the upper waters fluctuated considerably; they were as high as 30 colony-forming units per 100 mL in the spring and were not detected in the winter. Water samples from depths of 4000 to 7000 m contained less than 0.1 luminous colony-forming unit per 100 mL. The apparent vertical stratification of two taxa of oceanic luminous bacteria may reflect not only differences in physiology, but also depth-related, species-specific symbiotic associations.

562. Ruby, Edward G. and James G. Morin (1979). Luminous Enteric Bacteria of Marine Fishes: A Study of Their Distribution, Densities, and Dispersion. *Appl. Environ. Microbiol.* 38(3):406-411.

Three taxa of luminous bacteria (*Photobacterium fischeri*, *P. phosphoreum*, and *Beneckea* spp.) were found in the enteric microbial populations of 22 species of surface- and midwater-dwelling fishes. These bacteria often occurred in concentrations ranging between  $10^5$  and  $10^7$  colony-forming units per milliliter of enteric contents. By using a genetically marked strain, it was determined that luminous cells entering the fish during ingestion of seawater or contaminated particles traversed the alimentary tract and survived the digestive processes. After excretion, luminous bacteria proliferated extensively on the fecal material and became distributed into the surrounding seawater. Thus, this enteric habitat may serve as an enrichment of viable cells entering the planktonic luminous population.

563. Sadovskaya, G. M. and V. S. Filimonov (1985). The Factors Determining the Diurnal Dynamics of Phytoplankton Bioluminescence. *Oceanology* (USSR) 25(5): 825-831 (Russian) :642-646 (English).

Measurements of the bioluminescence intensity of plankton samples from a natural phytoplankton community reveal the extent to which bioluminescence is inhibited by daylight. The energy of bioluminescence in the absence of inhibition by light is proportional to the number of luminescing organisms at any time of day. The diurnal variation in bioluminescence is shown to be governed by the specific luminescence energy of the dominant species in the community.

564. Saito, T., M. Fukuda and S. Taguchi (1984). Bioluminescence of Cypridina III. Interpretation of Luminous Substrate Site in Labrum Gland. *Zool. Sci.* (Tokyo) 1(6):983.

**ABSTRACT.** Three types of cells occur in the labrum gland of *Cypridina* (*Vargula*) *hilgendorffii*—one with small, electron-dense granules, one with large electron-light granules, and one containing a mixture of both types of granules. Fluorescence microscopy shows that luminescent activity corresponds to the cell with small electron-dense granules. It is concluded that this cell contains luciferin.

565. Sai'nikov, N. V., S. E. Medvedeva, V. N. Petushkov, and I. I. Gitel'zon (1981). Electron-Microscopic Investigation of Structure of

Luciferase of Luminous Bacteria. *Dokl. Akad. Nauk SSSR* 261(5) :1254-1256 (Russian) :217-219 (English).

Molecular weights of luciferases from three bacterial species were determined. The physical structure of the molecule in all three cases was found to be a globule of 9-10 nm diameter. The globules were dispersed in two species, both mesophilic, and aggregated in one, which was psychrophilic. These physical differences may account for observed kinetic differences.

566. Satterlie, Richard A., Peter A. V. Anderson and James F. Case (1980). Colonial Coordination in Anthozoans: Pennatulacea. *Mar. Behav. Physiol.* 7:25-46.

Morphological and physiological evidence from five species of pennatulid octocorals indicates that a through-conducting colonial nerve net controls colony-wide responses including polyp withdrawal, bioluminescence and rachidial contraction. This nerve net is synaptic and located in the ectoderm and mesoglea of the colonial tissue. Nerve net impulses recorded extracellularly, show initial increases in conduction velocity during repetitive stimulation which promote facilitation of effectors. The response-amplitude of these effectors is frequency dependent. Bridge experiments suggest that interneural facilitation may contribute to the conduction velocity changes. Photometric measurements with concurrent electrophysiological recordings reveal that bioluminescence is under the control of the colonial nerve net. Luminescent responses show a frequency-dependent facilitation similar to that of other effectors. These physiological data, together with morphological data on the location and shape of autozooid photocytes, suggest that the photocytes may be modified circular or radial muscle cells. A second through-conducting colonial system was detected in three pennatulid species; the function of this system, however, was not evident.

567. Schröder-Lorenz, Angela and Ludger Rensing (1986). Circadian Clock Mechanism and Synthesis Rates of Individual Protein Species in *Gonyaulax polyedra*. *Comp. Biochem. Physiol.* 85B(2):315-323.

The dinoflagellate *Gonyaulax polyedra* synthesized RNA with significantly different rates during a circadian period under constant light. However, inhibition of RNA synthesis by 2 hr pulses

of actinomycin D did not phase shift the glow rhythm in a phase-dependent manner. Altered ambient temperatures (17–25°C) changed the phase of the protein synthesis rhythm as well as of the phase response curve to the protein synthesis inhibitor anisomycin. This confirmed the postulated relationship between the phase of maximal phase shifts and that of protein synthesis maximum. In phase with the maximum of total protein synthesis several protein species showed maximal rates of synthesis as shown by two-dimensional gel electrophoresis.

568. Seliger, Howard H. (1987). The Evolution of Bioluminescence in Bacteria. *Photochem. Photobiol.* 45(2):291–297.

Individuals of aerobic, saprophytic bacterial species, encountering a changing environment in which they were regularly exposed to periods of severe hypoxia, would have gained a major selective advantage in fatty acid metabolism if a mutation in a flavoprotein oxygenase permitted them to oxidize accumulated C<sub>8</sub>–C<sub>18</sub> aliphatic aldehydes to fatty acids at oxygen concentrations below which the cytochrome oxidase mediated electron transport pathway became inhibited. Such mutants, able to continue to metabolize exogenous lipid fatty acids under hypoxia, might have outproduced their wild type ancestors. Colonies of those mutants which utilized reduced flavin mononucleotide (FMNH<sub>2</sub>) as the flavin cofactor would have been luminous, owing to the fortuitous coincidence that the aldehyde oxygenation resulted in an enzyme-flavin excited electronic state which emitted blue light with a high fluorescence yield. If this accidental "proto-bioluminescence" were initially of sufficient brightness to have elicited phototactic responses in nearby motile organisms, increasing thereby detrital food sources or the potential for dispersal and colonization for the bacteria, a new and completely different selective advantage, that of bioluminescent signalling, would have arisen from the original metabolic function. This is the biochemical analog of Darwin's principle of functional change in structural continuity. It is proposed that bacterial luciferase, the FMNH<sub>2</sub>-oxygenase in luminous bacteria, was such a mutation. The present ubiquitous distributions of luminous bacterial species in marine waters, on the surfaces of marine animals and as symbionts in the specialized light organs and digestive tracts of many fish species have resulted from subsequent environmental selection and optimization

for this original protobioluminescent reaction. By extension it is suggested whereas "proto-bioluminescence" arose in many species independently whenever metabolic oxygenation of a substrate resulted in an adventitiously efficient chemiluminescence, the function of bioluminescence arose only upon favorable interaction between the "proto-bioluminescence" and its ecosystem.

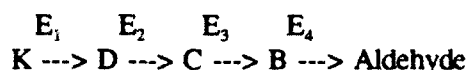
569. Seliger, Howard H. and William H. Biggley (1982). Optimization of Bioluminescence in Marine Dinoflagellates. *EOS* 63(45):945.

**ABSTRACT.** The total light emission upon mechanical stimulation to exhaustion (TMSL) is species-specific in dinoflagellates and varies from 10<sup>7</sup> to 10<sup>11</sup> photons per cell. The ratio of TMSL per cell to cell surface area is constant at about 10<sup>12</sup> photons per cm<sup>2</sup>. Thus predators disturbing only a part of the cell wall are subject to a constant light shock exposure, even though only part of the microsources may fire. This response saves energy for the cell and suggests that the spectral emission is optimized to match the predator's visual spectral sensitivity.

570. Shenderov, A. N. and L. Yu. Popova (1980). The Way of Synthesis of Luciferase Aldehyde Factor in *Photobacterium mandapamensis* and the Influence of Aldehyde Precursors on the Luminescence Development. *Genetika* 16(6):1109–1112 (Russian).

It is shown for the first time that the synthesis of luciferase-aldehyde factor has four successive stages. Aldehyde-dependent dark mutants of *Photobacterium mandapamensis* are used as a model. It is found that when two mutants grow on a solid medium together, one mutant stimulates the light sensitivity of the other mutant. Like the syntrophy test, the present test may be used to elucidate in what mutant the early stage of aldehyde factor synthesis is blocked. All the collection of aldehyde-dependent mutants is divided into four groups. The mutants of the first group do not stimulate the luminescence of mutants from other groups, but they increase luminescence under the influence of metabolites excreted by all other mutants. The mutants of the second group stimulate the luminescence of mutants from the first group only. The mutants of the third group stimulate the luminescence of mutants from first and second groups. The mutants of the fourth group increase the luminescence of all other mutants. On the

basis of the data obtained the following scheme of the luciferase-aldehyde factor synthesis is suggested:



It is observed that the nearer to the terminal stage the synthesis of aldehyde factor is blocked, the smaller amount of luciferase is synthesized in this mutant. Therefore, it may be supposed that precursors of aldehyde factor take part in the regulation of luciferase synthesis.

571. Shenderov, A. N. and L. Yu. Popova (1982). Genetic Investigations of *Photobacterium leiognathi*. V. Dynamics of the Synthesis of the Aldehyde Factor-the Main Substrate of Luciferase, *Sov. Genetics* 18(8) :1283-1288 (Russian) :956-960 (English).

It was shown on dark and dim mutant strains with blocked synthesis of the cell-aldehyde factor (the main substrate of luciferase) that the aldehyde-synthesizing enzyme can be synthesized both in coordination and out of coordination with luciferase. An analysis was made of the dynamics of the development of luminescence in aldehyde-dependent mutants, and it was established that some of the aldehyde-synthesizing enzymes may not be involved in the luciferase operon. Precursors of the aldehyde factor and an autoinducer, which is synthesized from precursors of the aldehyde factor, participate in the regulation of the synthesis of enzymes of the fluorescent system. The ratio of the concentrations of the autoinducer and precursors of the aldehyde factor determines either the coordinated or the uncoordinated regulation of the dynamics of the synthesis of luciferase and the aldehyde-synthesizing enzymes during the process of periodic culturing. The main role in the coordinated work of the operons coding the enzyme of the luminescent system is played by the autoinducer of luminescence.

572. Shenderov, A. N., L. Yu. Popova and I. Yu. Videletz (1982). Regulation Mechanisms of Enzyme Synthesis in the *Ph. leiognathi* and *B. harveyi* Luminescent Systems. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 251-273.

Studies of the effects of metabolically active chemicals on the kinetics of the luminescence reaction suggest that three separate catabolic operon systems

control the reaction. One controls synthesis of the autoinducer, a second synthesis of luciferase and the aldehyde-synthesizing enzymes, and the third repressor synthesis. The responses of the luminescence systems of different bacterial species to the controlling chemicals differ depending on the ecological niches occupied by the species. Bacterial growth and luminescence systems are suggested to be independent.

573. Shenderov, A. N., I. Yu. Videlets and L. Yu. Popova (1980). Influence of Amino Acids on the Induction of the Luminescence System of *Photobacterium belozerskii*. *Appl. Biochem. Microbiol.* 16(2) :162-171 (Russian) :117-125 (English).

The dynamics of the changes in the luminescence intensity of *Photobacterium belozerskii* growing in different media have been investigated. It has been shown that the luminescence intensity varies during the growth of the luminous bacterial cells by two to four orders of magnitude, depending on the composition of the culture medium. The addition of exogenous myristic aldehyde to the bacterial suspension at the time of the measurement of the luminescence results in a decrease in the luminescence intensity. The extent of the decrease was practically independent of the luminescence intensity. The time for the beginning of the increase in the luminescence intensity depended on the composition of the culture medium. The addition of arginine, proline, and asparagine to the culture medium resulted in a decrease in the latent period and a simultaneous increase in the luminescence intensity by factors of 30, 10, and 5-10, respectively. Arginine and proline added to the minimal medium at the time of the increase in the luminescence of *P. belozerskii* caused increases in the rate of the biosynthesis of the enzymes of the luminescence system by factors of 32 and 10, respectively. Under the combined action of these amino acids the rate of the biosynthesis of luciferase increased 630-fold. The possible mechanisms and causes of the observed phenomena are discussed.

574. Shilo, M. and T. Yetinson (1979). Physiological Characteristics Underlying the Distribution Patterns of Luminous Bacteria in the Mediterranean Sea and the Gulf of Elat. *Appl. Environ. Microbiol.* 38(4):577-584.

Physiological characteristics of luminous bacteria isolated from the Mediterranean and Gulf of Elat were compared to determine their relationship to the specific seasonal and geographic distribution patterns

of these bacteria. The effects of temperature on growth rate and yield, relative sensitivity to photooxidation, resistance to high salt concentration (8%), and ability to grow in nutrient-poor conditions appear to control these patterns. The winter appearance of *Photobacterium fischeri* and the succession of winter and summer types of *Beneckeia harveyi* in the eastern Mediterranean are explained by different temperature requirements for growth. Sensitivity to photo-oxidation explains the disappearance of *P. leiognathi*, present in the main body of the Gulf of Elat throughout the year, from the shallow coastal strip. *B. harveyi* is present in this coastal strip which is higher in nutrients than the open waters. Competition experiments between *B. harveyi* and *P. leiognathi* in batch and continuous culture indicate that the oligotrophic *P. leiognathi* is outcompeted by *B. harveyi* in rich and even in relatively poor media. The distribution pattern found in the Bardawil hypersaline lagoon is explained by selection of salinity-resistant mutants of *B. harveyi* from the Mediterranean Sea.

575. Shimomura, Osamu (1980). Chlorophyll-Derived Bile Pigment in Bioluminescent Euphausiids. *FEBS Letters* 116(2): 203-206.

Light emission in the euphausiid shrimp *Meganctiphanes norvegica* is due to oxidation of a photoprotein in the presence of a very unstable fluorescence substance designated "F," which both catalyzes the reaction and acts as emitter (emission and fluorescence maxima both are 476 nm). Evidence suggests that "F" is a bile pigment-type compound derived from chlorophyll, in contrast to most such compounds which are derived from heme.

576. Shimomura, Osamu (1982). Mechanism of Bioluminescence. In *Chemical and Biological Generation of Excited States*, W. Adams and G. Cilento, eds., New York: Academic Press, pp. 249-276.

Well-known bioluminescent systems are tabulated. The structures of six known luciferins are depicted. Energy-producing reactions and oxidation mechanisms for many organisms are discussed, along with the presence of chromophores in some organisms and mechanisms involving intermolecular energy transfer to shift the emitted wavelength.

577. Shimomura, Osamu (1983). Bioluminescence. *Photochem. Photobiol.* 38(6):773-779.

This paper reviews approximately 150 papers that were published in 1982 and the first half of 1983 or were in press. In the last several years, there has been a steady increase in the number of papers dealing with various aspects of the analytical application of bioluminescence. Papers in this category now exceed one-third of all the papers presently surveyed. In regard to papers dealing with more fundamental aspects (about 100 papers), 40% of those papers are related to bacterial bioluminescence, making them the largest group of papers, followed by the groups of papers related to the firefly system and dinoflagellate bioluminescence (15%, respectively). The chemical mechanisms of bioluminescence have been reviewed by several authors. Papers on other topics are grouped.

578. Shimomura, Osamu (1985). Bioluminescence in the Sea: Photoprotein Systems. In *Physiological Adaptations of Marine Animals (Soc. Exp. Biol. Symp. 39:351-372)*, M. S. Laverack, ed., Society for Experimental Biology, Cambridge, UK, pp. 351-372.

Photoproteins are the primary reactants of the light-emitting reactions of various bioluminescent organisms. A photoprotein emits light in proportion to its amount, like a luciferin, but its light-emitting reaction does not require a luciferase. There are about 24 types of bioluminescent organisms for which substantial biochemical knowledge is presently available and about one third of them involve photoproteins. Most photoproteins are found in marine organisms. There are various types of photoproteins: the photoproteins of coelenterates, ctenophores and radiolarians require  $\text{Ca}^{2+}$  to trigger their luminescence; the photoproteins of the bivalve *Pholas* and of the scale worm appear to involve superoxide radicals and  $\text{O}_2$  in their light-emitting reactions; the photoprotein of euphausiid shrimps emits light only in the presence of a special fluorescent compound; the photoprotein of the millipede *Luminodesmus*, the only known example of terrestrial origin, requires ATP and  $\text{Mg}^{2+}$  to emit light. The  $\text{Ca}^{2+}$ -sensitive photoproteins of coelenterates have been most frequently studied and most widely used. Therefore, they are overwhelmingly popular compared with other types. All coelenterate photoproteins, including aequorin, halistaurin, obelin, and phialidin, have relative molecular masses close to 20,000, contain an identical functional group and emit blue light in aqueous solution when a trace of  $\text{Ca}^{2+}$  is added, in the presence or absence of molecular oxygen. Aequorin contains an oxygenated form of

coelenterazine in its functional group. When  $\text{Ca}^{2+}$  is added, aequorin decomposes into three parts, i.e., apo-aequorin, coelenteramide and  $\text{CO}_2$ , accompanied by the emission of light. Apo-aequorin can be reconstituted into active aequorin indistinguishable from the original sample by incubation with an excess of coelenterazine in a buffer containing 5 mM-EDTA and a trace of 2-mercaptoethanol, even at  $0^\circ\text{C}$ . Thus, aequorin and other coelenterate photoproteins can be luminesced and recharged repeatedly. The regeneration of coelenterate photoproteins in this manner probably takes place in vivo, utilizing stored coelenterazine.

579. Shimomura, Osamu (1986). Bioluminescence of the Brittle Star *Ophiopsila californica*. *Photochem. Photobiol.* 44(5):671-674.

The light-emitting principle of the brittle star *Ophiopsila californica* has been isolated and purified. It was found to be a green-fluorescent photoprotein (molecular weight 45,000) which emits green light ( $\lambda_{\text{max}}$  500 nm) when  $\text{H}_2\text{O}_2$  is added, independently of the presence or absence of  $\text{O}_2$ . The green fluorescence (emission maximum 500 nm, excitation maximum 440 nm) spectrally coincided with the  $\text{H}_2\text{O}_2$ -triggered luminescence, indicating that the green-fluorescent chromophore is the light-emitter of the photoprotein luminescence.

580. Shimomura, Osamu (1986). Isolation and Properties of Various Molecular Forms of Aequorin. *Biochem. J.* 234:271-277.

The photoprotein aequorin emits light by an intramolecular reaction when a trace of  $\text{Ca}^{2+}$  is added. The samples of aequorin that were purified by the conventional methods of column chromatography were separated by high-performance liquid chromatography into eight molecular forms (isoequorins), which were designated aequorins A-H. Aequorins A, C, and F were obtained in crystalline states. A wide range of properties were studied with aequorins A-F, which were essentially pure. These six isoequorins showed relatively small differences in their spectroscopic properties, but their values of  $0.1\% A_{1\text{ cm}, 280}$  were found to be close to 3.0, about 10% more than the previously reported value of 2.70-2.71 that was obtained with the samples of conventionally purified aequorin. The  $M_r$  values ranged from 20100 (aequorin F) to 22800 (aequorin A), the luminescence activities ranged from  $4.35 \times 10^{15}$  photons/mg (aequorin A) to  $5.16 \times 10^{15}$  photons/mg (Aequorin F),

and the first-order reaction rate constants of luminescence ranged from  $0.95 \text{ s}^{-1}$  (aequorin A) to  $1.33 \text{ s}^{-1}$  (aequorin F). As regards sensitivity to  $\text{Ca}^{2+}$ , aequorin D was the most sensitive, having a sensitivity about 0.4-0.5 pCa unit above that of the least sensitive kind (aequorin A).

581. Shimomura, Osamu (1986). Rechargeable Energy Storage in Nature: Coelenterate Photoproteins. In *Natural Products and Biological Activities*. Hiroo Imura, Toshio Goto, Takashi Murachi and Terumi Nakajima, eds., Tokyo: University of Tokyo Press, pp. 33-44.

The term, "photoprotein," is defined. Photoproteins are classified into four groups: (1) euphausiid photoproteins, which emit light in the presence of a fluorescent compound and  $\text{O}_2$ ; (2) photoproteins that emit light in the presence of superoxide radical  $\text{O}_2^-$  and  $\text{O}_2$ ; (3) the photoprotein of the millipede *Luminodesmus* that emits light when ATP is added in the presence of  $\text{Mg}^{2+}$  and  $\text{O}_2$ ; and (4) coelenterate photoproteins that emit light when  $\text{Ca}^{2+}$  is added. The history of the discovery of aequorin and extraction and purification procedures are given. Its chemical and physical properties are tabulated and discussed. The structure of its active group (coelenterazine) is depicted and its relation to *Cypridina* luciferin is discussed, along with the widespread occurrence of coelenterazine. A model for the regeneration of aequorin after discharge is presented. Other coelenterate photoproteins are discussed and the spectral emission maxima of several are tabulated. Stimulation of bioluminescence and energy transfer in living coelenterates are discussed.

582. Shimomura, Osamu, Shoji Inoue, Frank H. Johnson and Yata Haneda (1980). Widespread Occurrence of Coelenterazine in Marine Bioluminescence. *Comp. Biochem. Physiol.* 65B:435-437.

Coelenterazine is a compound having a key role in the light-emitting process of bioluminescent coelenterates. Present evidence concerning the occurrence of coelenterazine and luciferase in other types of marine organisms establishes that coelenterazine is required for bioluminescence of various, distantly related, types of organisms such as squids, shrimps, and fishes. In the bioluminescent shrimps and fishes, coelenterazine occurs most abundantly along the digestive tract, suggesting the

possibility that this compound derives from ingested food.

583. Shimomura, Osamu and Frank H. Johnson (1979). Chemistry of the Calcium-Sensitive Photoprotein Aequorin. In *Detection and Measurement of Free  $\text{Ca}^{2+}$  in Cells*, C. C. Ashley and A. K. Campbell, eds., Amsterdam (Netherlands): Elsevier Biomedical Press, pp. 73-83.

Here the recent chemistry of the calcium-sensitive photoprotein aequorin is described, together with the structure of the prosthetic group active in light emission. The most recent physical and kinetic properties of the photoprotein are also collated.

584. Shimomura, Osamu and Frank H. Johnson (1979). Comparison of the Amounts of Key Components in the Bioluminescence Systems of Various Coelenterates. *Comp. Biochem. Physiol.* 64B:105-107.

The contents of luciferase, photoprotein, coelenterazine and its enol-sulfate in five species of bioluminescent coelenterates were assayed and compared. Hydrozoans *Aequorea* and *Halistaura* contained photoprotein plus very small amounts of coelenterazine enol-sulfate and luciferase activity, but no free coelenterazine. The anthozoans *Ptilosarcus*, *Cavernularia* and *Renilla* contained luciferase and coelenterazine as well as its enol-sulfate, but very little or no photoprotein. Most of the coelenterazine existed in a stabilized form bound to a Ca-binding protein.

585. Shimomura, Osamu and Akemi Shimomura (1984). Effect of Calcium Chelators on the  $\text{Ca}^{2+}$ -dependent Luminescence of Aequorin. *Biochem. J.* 221:907-910.

The luminescence of aequorin, a useful tool for studying intracellular  $\text{Ca}^{2+}$ , was recently found to be inhibited by the free EDTA and EGTA that are present in calcium buffers. In this study they examined the effect of the free forms of various chelators in the calibration of  $[\text{Ca}^{2+}]$  with aequorin. Free EDTA and EGTA in low-ionic-strength solutions strongly inhibited the  $\text{Ca}^{2+}$ -triggered luminescence of aequorin, causing large errors in the calibration of  $[\text{Ca}^{2+}]$  (approx. 2 pCa units), whereas in solutions containing 150 mM-KCl, errors were relatively small (0.2-0.3 pCa units). Citric acid in low-ionic-strength solutions and [(carbamoylmethyl) imino]diacetic acid in high-ionic-strength solutions showed no inhibition and

did not cause detectable error in the calibration of  $[\text{Ca}^{2+}]$ , indicating that they are better chelators than EDTA and EGTA for use with aequorin.

586. Shimomura, Osamu and Akemi Shimomura (1985). Halistaurin, Phialidin and Modified Forms of Aequorin as  $\text{Ca}^{2+}$  Indicators in Biological Systems. *Biochem. J.* 228:745-749.

Two kinds of aequorin-type photoproteins, i.e., halistaurin and phialidin, and four kinds of modified forms of aequorin, i.e., products of acetylation, ethoxycarbonylation, fluorescamine-modification, and fluorescein labelling, were prepared. The modified forms of aequorin were more sensitive to  $\text{Ca}^{2+}$  than was aequorin in their  $\text{Ca}^{2+}$ -triggered luminescence reactions, whereas halistaurin and phialidin were less sensitive. The emission maxima of luminescence were all within a wavelength range 450-464 nm, except for fluorescein-labelled aequorin, which emitted yellowish light ( $\lambda_{\text{max}}$  520 nm). A new technique of measuring  $\text{Ca}^{2+}$  concentration is suggested.

587. Smayda, Theodore J. (1980). Phytoplankton Species Succession. In *The Physiological Ecology of Phytoplankton*. I. Morris, ed., Berkeley (California): University of California Press, pp. 493-570.

Section 14.8.4 of this article describes the bioluminescent bays of Puerto Rico and Jamaica as nearly continuous blooms of *Pyrodinium bahamense*, representing the closest approximation to a climax community manifested in the phytoplankton. Previous studies on Bahia Fosforescente and Oyster Bay are summarized, including a physical model for maintaining the high dinoflagellate populations. Ignorance is expressed on the reasons for the very small numbers of diatoms found, even though the growth-supporting potential of bay waters for diatoms is favorable.

588. Somiya, Hiroaki (1979). "Yellow Lens" Eyes and Luminous Organs of *Echiostoma barbatum* (Stomiatoidei, Melanostomiidae). *Jap. J. Ichthyol.* 25(4):269-272.

The deep-sea mesopelagic fish *Echiostoma barbatum* has yellow lenses in its eyes and four different kinds of photophores. It emits light in both red and blue wavelengths (from different organs). The blue light is used for counterillumination and may also be used for luminescent silhouetting, or rendering a visible outline for unknown purposes. The red light

may be used to detect prey without being seen by prey or predators and/or for intra-specific communication. The yellow eye lens increases sensitivity to long-wavelength light and, coupled with red-sensitive rods in the retina, allows the fish selectively to see dim red signals. This interpretation supports the suggested uses for the red emission.

589. Somiya, Hiroaki (1981). On the Bacterial-Associated Light Organ in *Chlorophthalmus*. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., Academic Press, New York, pp. 561-567.

The myctophid fish *Chlorophthalmus* contains a small neurally-controlled bacterial light organ forming a doughnut around the anus. It consists of a luminous body, reflector, and chromophores. In the luminous body the bacteria are associated with special cells that may provide nutrition. The bacteria may be *Photobacterium phosphoreum*. Peak light emission is at 475 nm.

590. Squire, James L. (1983). Abundance of Pelagic Resources off California, 1963-1978, as Measured by an Airborne Fish Monitoring Program. NOAA Technical Report NMFS SSRF-762.

From September 1962 through December 1978 commercial aerial fish-spotter pilots operating off southern and central California and northern Mexico, maintained a flight log indicating the geographical areas searched and an estimate of the quantity of pelagic species observed. These flight logs were analyzed for quantities of species observed per block area (10-ft. longitude by 10-ft. latitude area). Flights were recorded as surveying all or a portion of 164,753 block areas. A total of 110,375 block areas were surveyed during the day and 54,378 during night operations. An annual index of apparent abundance (arbitrary values) was computed for each of the major species observed, both for day and night aerial observations from selected geographical areas and for total observations. The index value computed is not directly comparable between species. During the night, fish-school identification was made by the bioluminescent characteristics of its shape or its behavioral response to a flash of light.

591. Squire, James L. and Howard Krumboltz (1981). Profiling Pelagic Fish Schools Using Airborne Optical

Lasers and Other Remote Sensing Techniques. *Mar. Tech. Soc. J.* 15(4):27-31.

Fish schools were located at night with an airborne low-light-level television camera system and identified by their characteristic bioluminescent shapes and behaviors in response to pulsed light from the aircraft. A picture of a bioluminescence-outlined anchovy school is shown.

592. Stahr, Norbert, Gerhard Holzapfel and Rüdiger Hardeland (1980). Phase Shifting of the *Gonyaulax* Clock by Puromycin. *J. Interdiscipl. Cycle Res.* 11(4):277-284.

Continuous treatment with high doses of puromycin suppresses the circadian rhythm of bioluminescence in *Gonyaulax polyedra*. When given in submaximal doses, which are inhibitory only in the third or fourth cycle, the antibiotic causes phase delays. At a higher dosage, pulse treatment in different phases results in a phase-response curve. Occurrence of phase-advance shifts and extent of delay shifts depends on pulse duration. Continuous treatment with a falsifier of transcription, 5-azacytidine, causes a reduction in bioluminescence, but does not delay the rhythm. Therefore, the role of protein synthesis in the *Gonyaulax* clock seems to be predominantly of post-transcriptional nature.

593. Stehling, Kurt R. (1980). An Undersea Radiation Detection Experiment Mission Report. National Oceanic and Atmospheric Administration Report, 4 December.

A detector called CYCLOPS, consisting of a cylinder with three photomultiplier tubes having nanosecond resolution and originally designed to detect neutrinos and Cerenkov radiation undersea, was used to detect bioluminescence during a dive on the manned submersible Johnson-Sea-Link off West End, Grand Bahama Island, on 21-22 October, 1980. High-bioluminescence activity was visually observed throughout the dive, but a 90% full moon saturated the detector above 1100 feet. From 1100 to 2000 feet, the maximum depth of the dive, bioluminescence was successfully recorded; the majority, however, was generated by the submersible itself. Bioluminescence signals could be successfully distinguished from Cerenkov signals by their kinetics as seen on an oscilloscope screen.

594. Steidinger, K. A., L. S. Tester and F. J. R. Taylor (1980). A Redescription of *Pyrodinium bahamense* var. *compressa* (Böhm) stat. nov. from Pacific Red Tides. *Phycologia* 19(4):329-337.

A toxic, chain-forming variety of the thecate dinoflagellate *Pyrodinium bahamense* from the Pacific Ocean is redescribed and the taxonomic characteristics that distinguish it from the Atlantic variety *P. bahamense* var. *bahamense* are given. The reasons for varietal rather than specific classification and previous descriptions under other names (now considered to be synonyms) are summarized. *P. bahamense* var. *compressa* forms luminous red tides in coastal waters of Papua New Guinea, Sabah, Brunei, the Persian Gulf, the Red Sea, the Andaman Sea, and the Pacific coast of Mexico.

595. Stepien, Carol A. and Richard C. Brusca (1985). Nocturnal Attacks on Nearshore Fishes in Southern California by Crustacean Zooplankton. *Mar. Ecol. Prog. Ser.* 25:91-105.

Adult nearshore fishes in large cages on the seafloor off southern California mysteriously died within 3 to 4 hours after sunset. Night diving observations showed that fishes were attacked by swarms of crustacean zooplankton, primarily the luminescent ostracod *Vargula tsujii* Kornicker & Baker 1977 (Myodocopida: Cypridinidae) and the isopod *Cirolana diminuta* Menzies 1962 (Cirolanidae), species previously identified as members of the southern California demersal zooplankton assemblage. Experiments using traps baited with live fishes showed that attacks occur year-round on many species of nearshore fishes, in both sandy and rocky habitats and on adults of both sexes more frequently than on juveniles. Ostracods were attracted to fishes first, attaching to their sides and opercula, but not alone causing serious injury. Cirolanid isopods later invaded the traps and were responsible for the fish deaths, usually through extensive gill damage. Both ostracods and isopods often invaded the gills and also often entered the body cavity through the anus, consuming gonads and liver. Laboratory maze experiments showed that ostracods are attracted to chemicals released from sexually mature fishes and by their own bioluminescence. Isopods are attracted to chemicals released by injured fishes, thus they may preferentially attack fishes initially injured by ostracods. *V. tsujii* also clustered around unrestrained fishes at night in situ; fishes resting near the seafloor periodically shook

off the ostracods and sometimes moved to other locations when surrounded by large numbers. Other fishes apparently avoid the ostracods by swimming higher into the water column, burying themselves in sand, or hiding in rock crevices. Emergent crustacean zooplankton may significantly influence nocturnal versus diurnal distributions and behavior of nearshore fishes. Surveys of commercial fishermen indicated that crustacean zooplankton also cause extensive damage to fishes caught in gill nets, often rendering a significant percentage of a catch unmarketable. Evolutionary and ecological aspects of the phenomenon are discussed.

596. Stiffey, Arthur V., David L. Blank and George I. Loeb (1985). An Inexpensive Solid-State Photometer Circuit Useful in Studying Bioluminescence. *J. Chem. Education* 62:360-361.

A new photometer circuit is described and a schematic is shown. The performance of the new circuit equals or exceeds that of older circuits at a fraction of the cost.

597. Sulzman, Frank M., Van D. Gooch, Keiichi Homma and J. Woodland Hastings (1982). Cellular Autonomy of the *Gonyaulax* Circadian Clock. *Cell Biophysics* 4:97-103.

Because of the long-term persistence of free-running circadian rhythms in populations of unicells, several investigators have considered, but not demonstrated, a possible role for intercellular interaction in maintaining synchrony between individual cells. The experiments described here were designed to test more critically the possibility that there is interaction between cells, including those possessing only small phase differences. None was detected; the bioluminescent glow of the mixed cultures matched the algebraic sum of the independent control cultures.

598. Sumida, Brian H. and James F. Case (1983). Food Recognition by *Chaetopterus variopedatus* (Renier): Synergy of Mechanical and Chemical Stimulation. *Mar. Behav. Physiol.* 9:249-274.

Food recognition and related behavior was studied in specimens of *Chaetopterus variopedatus* (Renier) housed in glass tubes in flowing seawater. Particulates and amino acids were added to the flow, mimicking food stimuli and water currents produced by the worm's fanning and were recorded with a

Doppler flow meter. Fanning duration was negatively correlated with feeding. Of amino acids tested, glycine and taurine significantly reduced fanning duration. Cellulose chromatography beads, a nonchemically enriched particulate food mimic, also significantly reduced fanning duration. However, neither particulate nor chemical stimuli were equal to plankton (*Gonyaulax polyedra*) in reducing fanning duration. When an ineffectively low concentration of glycine was presented simultaneously with chromatography beads, at one-hundredth the particle concentration of plankton, fanning duration shortened to periods characteristic of responses to plankton. These results suggest that both particulate (tactile) and chemical stimuli are important in the recognition of food. Synergy between the two senses appears necessary to effect a maximum feeding response. Long-term (24-hour) exposure to low-concentration water-soluble petroleum fractions (WSF) caused desensitization of chemoreception in adult *C. variopedatus*. Short-term exposure to WSF had no effect on fanning duration. Dilute acetic acid solution evoked simultaneous bioluminescence and rejection responses.

599. Suzuki, Kenzi, Toshio Kaidoh, Masayuki Katagiri and Takashi Tsuchiya (1983). O<sub>2</sub> Incorporation into a Long-Chain Fatty Acid during Bacterial Luminescence. *Biochim. Biophys. Acta* 722:297-301.

The bioluminescence-dependent oxidation of a long-chain fatty aldehyde catalyzed by luciferase from *Photobacterium phosphoreum* has been studied in 18O<sub>2</sub> experiments. The results show the incorporation of one atom of molecular oxygen into the product, the corresponding fatty acid. This incorporation is not the result of exchange of 18O<sub>2</sub> with the aldehyde prior to oxidation to the acid, thereby indicating that the bacterial luciferase catalyzes an aldehyde monooxygenase reaction which is coupled with bioluminescence.

600. Swales, Lesley S., Peter J. Herring and Nancy J. Lane (1986). Unusual Membranous Structures in the Bioluminescent Cells of the Deep Sea Crustacean *Scina*. *Biol. Cell*. 57:53-62.

Many oceanic amphipod crustaceans are luminescent, with the luminous cells (photocytes) restricted to certain defined sites. The photocytes present in the deep-sea genus *Scina* have been investigated ultrastructurally and are found to exhibit

a number of peculiar structural features. These include an unusual system of channels of different sizes, into which substances may pass, arrays of membranes in the form of extensive networks associated with dense material which appears to arise from the endoplasmic reticulum, and an array of dense bodies. These cells are often in close spatial association with cells possessing phenomenally extensive Golgi membranes, which may be related to the photocytic activity. The photocytes become brightly fluorescent after bioluminescence and the differences in the morphology of fluorescent and nonfluorescent photocytes have been investigated. The results have been interpreted in the context of a cycle of events linking the resting state with bioluminescent activity.

601. Sweeney, Beatrice M. (1979). The Organisms, Opening Remarks. In *Toxic Dinoflagellate Blooms*. Dennis L. Taylor and Howard H. Seliger, eds., North Holland/New York: Elsevier, pp. 37-40.

Unique physical and physiological characteristics of dinoflagellates are discussed. A distinction is made between blooms and red tides, and possible biological and chemical factors that could lead to the formation of red tides are outlined. Evidence supporting or opposing the theorized mechanisms is presented.

602. Sweeney, Beatrice M. (1979). Bright Light Does Not Immediately Stop the Circadian Clock of Bioluminescence. *Plant Physiol.* 64:341-344.

Circadian rhythms in acid-stimulated bioluminescence and cell division are observed for at least 16 days in bright continuous light (4.5 mW/cm<sup>2</sup> or 20,000 lux). The photosynthesis rhythm also fails to stop immediately upon transfer of cell suspensions to bright light. After about 4 weeks under these conditions, all rhythms were observed to damp out. In cells transferred from bright light to continuous darkness, the rhythms were reset to about circadian hour 12 to 14, the phase of the beginning of a normal night.

603. Sweeney, Beatrice M. (1979). Circadian Rhythmicity in the Morphology of *Pyrocystis fusiformis* (Pyrrophyta). *J. Phycol.* 15(S):23.

**ABSTRACT.** A circadian rhythm of chloroplast deployment in *Pyrocystis fusiformis* is identified. Like those of bioluminescence and cell division, it persists in constant light and temperature conditions.

604. Sweeney, Beatrice M. (1979). The Bioluminescence of Dinoflagellates. In *Biochemistry and Physiology of Protozoa*, Vol. 1, M. Levandowski and S. H. Hunter, eds., New York: Academic Press, pp. 287-306.

Known bioluminescent species of dinoflagellates and selected nonluminous species are tabulated. Some species have both luminous and nonluminous strains. Flash characteristics are discussed and flash intensities and peak emission wavelengths of selected species are tabulated. Photoinhibition of the mechanically stimulated flash in photosynthetic dinoflagellates is discussed, but no photoinhibition in nonphotosynthetic species is found. Chemical and electrical stimulation, spontaneous flashing and glows are also discussed. The biochemistry of the light-producing reaction is outlined and the chemical characteristics of the luciferin, luciferase and soluble and particulate bioluminescent fractions are presented. Circadian rhythms in photosynthetic luminous dinoflagellates are summarized, but none are found in nonphotosynthetic species. A theory of the adaptive value of luminescence in dinoflagellates is presented.

605. Sweeney, Beatrice M. (1980). The Circadian Rhythms in Bioluminescence and Organellar Movements in the Large Dinoflagellate, *Pyrocystis fusiformis*. *Eur. J. Cell Biol.* 22 (1):495.

**ABSTRACT.** *Pyrocystis fusiformis* shows changing morphology and chloroplast migration from the periphery of the cell during the day to its center at night. Bioluminescence is confined to a spherical region next to the nucleus during the day and disperses to the periphery at night. It is 10-50 times brighter at night than during the day. These movements exhibit a circadian rhythm in constant light.

606. Sweeney, Beatrice M. (1980). Intracellular Source of Bioluminescence. *Int. Rev. Cytology* 68:173-195.

What is known about the physical sources of bioluminescence within the cell, in those organisms whose light emission is intracellular, is summarized. Only in fireflies and polychaete scaleworms is the luminous organelle well established. In dinoflagellates, luminous microsources appear to be electron-dense membrane-bound particles in the peripheral cytoplasm, but this observation is unconfirmed. Luminescence in extracts from coelenterates is associated with vesicular

particles called lumisomes, but these structures have not been identified with certainty in sections of photogenic tissue. In fish and squid, subcellular sources of luminescence have been suggested only through speculation and analogy. Indeed, in the many of these organisms that extrude luminous secretions, the glandular cells producing the secretions are, at best, only tentatively identified.

607. Sweeney, Beatrice M. (1980). Whirling Whips and Firey Plants, a Review of an Astonishing Group. *Abstr., 8th Ann. Meet. Am. Soc. Photobiol.*, p. 105.

**ABSTRACT.** Dinoflagellates as a group are taxonomically defined and their morphology, reproductive mechanisms and feeding habits are described. They exhibit a number of circadian rhythms, including bioluminescence and many possess the ability to emit light upon stimulation, an ability unique among photosynthetic organisms. The flash, which takes place in about 0.1 sec and has a spectral emission peak at about 475 nm, is preceded by an unusual negative action potential. Light emission can occur in soluble extracts or particle-bound fractions. Some, but not all, species contain a luciferin-binding protein in addition to luciferin and luciferase.

608. Sweeney, Beatrice M. (1981). Circadian Timing in the Unicellular Autotrophic Dinoflagellate, *Gonyaulax polyedra*. *Ber. Deutsch. Bot. Ges.* 94:335-345.0

The theory of regulation of circadian rhythms by means of an internal biological "clock" is presented. Supporting evidence of clock-controlled rhythms in a variety of organisms is outlined. Three rhythms in *Gonyaulax polyedra*—cell division, photosynthesis and bioluminescence—are discussed in detail in an attempt to elucidate the clock mechanism. Experiments in which inhibitors have been used as probes provide evidence that proteins synthesized on 80S but not on 70S ribosomes are components of the "clock." The evidence is less clear that the mechanism is a limit cycle of which the components are membrane transport activity across organellar membranes and the concentrations of the ions transported. Evidence is presented, however, that strongly suggests that membranes and their components are important in temporal regulation.

609. Sweeney, Beatrice M. (1981). The Circadian Rhythms in Bioluminescence, Photosynthesis and

Organelle Movements in the Large Dinoflagellate, *Pyrocystis fusiformis*. In *International Cell Biology 1980-1981*, H. G. Schweiger, ed., New York: Springer Verlag, pp. 807-814.

The marine dinoflagellate, *Pyrocystis fusiformis*, isolated by the author from the Halmehara Sea in S. E. Asia, is 800-100µm in length with a large vacuole. In addition to changing morphology as it progresses through the cell cycle, this organism shows chloroplast migration from the periphery of the cell during the day to the center at night. During the day, bioluminescence is confined to the central region of the cell and disperses to the periphery at night. Light emitted at night is 10-50 × brighter than during the day when the cells are stimulated to bioluminescence by the addition of acid. Photosynthesis reaches a maximum in the middle of the day. Bioluminescence, <sup>14</sup>C fixation at saturating light, chloroplast movement and cell stages have been monitored in cells transferred to constant conditions, either continuous light or darkness, at the end of the day. In a constant environment, a circadian rhythm in bioluminescence, photosynthesis, chloroplast movement, appearance of a central yellow sphere and cell division could be demonstrated for at least five cycles. Examination of *P. fusiformis* fixed for electron microscopy at different times of day, confirmed the chloroplast migration and provided details of other morphological changes.

610. Sweeney, Beatrice M. (1981). Variations in the Bioluminescence per Cell in Dinoflagellates. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis, Minnesota: Burgess Publishing Co., pp. 90-94.

Circadian rhythms of bioluminescence and sensitivity to mechanical stimulation in *Pyrocystis fusiformis* are identified. Depletion of phosphate, nitrate and iron and age of cultures have little effect on bioluminescence emission. However, lowering the ambient temperature and increasing total irradiance during the preceding photophase strongly increase bioluminescence.

611. Sweeney, Beatrice M. (1982). Interaction of the Circadian Cycle with the Cell Cycle in *Pyrocystis fusiformis*. *Plant Physiol.* 70:272-276.

Dividing pairs or single cells of the large dinoflagellate, *Pyrocystis fusiformis* Murray, were isolated in capillary tubes and their morphology was observed over a number of days, either in a light-dark

cycle or in constant darkness. Morphological stages were correlated with the first growth stage, G<sub>1</sub>; DNA synthesis, S; the second growth stage, G<sub>2</sub>; mitosis, M; and cytokinesis, C, segments of the cell division cycle. The S phase was identified by measuring the nuclear DNA content of cells of different morphologies by the fluorescence of 4', 6-diamidino-2-phenylindole dichloride. Cells changed from one morphological stage to the next only during the night phase of the circadian cycle, both under light-dark conditions and in continuous darkness. Cells in all segments of the cell division cycle displayed a circadian rhythm in bioluminescence. These findings are incompatible with a mechanism for circadian oscillations that invokes cycling in G<sub>0</sub>, a hypothesized side loop from G<sub>1</sub>. All morphological stages, not only division, appear to be phased by the circadian clock.

612. Sweeney, Beatrice M. (1982). Microsources of Bioluminescence in *Pyrocystis fusiformis* (Pyrophyta). *J. Phycol.* 18(3):412-416.

The large dinoflagellate, *Pyrocystis fusiformis* Murray, emits bioluminescence on stimulation with dilute acid. The bioluminescence can be seen in the light microscope to originate in a spherical region just distal to the nucleus during the day and appears as a persistent glow which can be localized in an orange-brown sphere. At night, the bioluminescence, in response to stimulation, is a bright flash from microsources scattered throughout the cytoplasm. The orange sphere can no longer be seen nor does a bioluminescent glow originate from this central region on stimulation. This difference in the position of intracellular bioluminescence between day and night has allowed the identification in electron micrographs of structures which correspond to the source of bioluminescence during the day. Light is emitted from a spherical mass of vesicles which contain electron-dense short rods with rounded ends, sometimes crossed by electron-transparent narrow bands. At night, these vesicles can be recognized in the peripheral cytoplasm. It is proposed that these vesicles are the structural counterparts of the microsources of bioluminescence in *P. fusiformis*.

613. Sweeney, Beatrice M. (1984). Circadian Rhythmicity in Dinoflagellates. In *Dinoflagellates*, David L. Spector, ed., New York: Academic Press, pp. 343-363.

"Circadian rhythm" is defined and the relevance of dinoflagellates as a study tool for circadian rhythms is established. Theories of the evolution and ecological significance of circadian rhythms are discussed. The circadian rhythms of photosynthesis, chloroplast structure and migration, phototaxis, vertical migration, motility, cell division, and bioluminescence are presented in detail.

614. Sweeney, Beatrice M. (1987). Bioluminescence and Circadian Rhythms. In *The Biology of Dinoflagellates* (Bot. Monogr. 21:269-281). F. J. R. Taylor, ed., Palo Alto, (California): Blackwell Scientific Publications, pp. 269-281.

Physical characteristics of dinoflagellate bioluminescence, including intensity, spectra and kinetics, for mechanically stimulated flashes and spontaneous glows, are given. Known luminous species are listed. Photoinhibition, the influence of temperature on bioluminescent emission, cross-reactions and biochemical and physiological mechanisms of light emission are discussed. The physical and chemical characteristics of luciferin, luciferase, and luciferin-binding protein are described. A possible function of bioluminescence in avoiding predation is mentioned. The circadian rhythms of bioluminescence are described and related to other rhythms, and possible chemical mechanisms for operating or regulating the intracellular clock are discussed.

615. Sweeney, Beatrice M. and Susan I. Folli (1984). Nitrate Deficiency Shortens the Circadian Period in *Gonyaulax*. *Plant Physiol.* 75:242-245.

The circadian rhythms in bioluminescence and photosynthesis in *Gonyaulax polyedra* suspended in unsupplemented seawater have been compared to the same rhythms in *f/2*, an enriched seawater medium. Cells suspended in seawater for 2 days in continuous light (450  $\mu\text{W}/\text{cm}^2$ ) showed significantly shorter circadian periods and lower amplitudes than did cells in *f/2* medium (a period of 22.2 hours as compared to 23.5 hours). Both period and amplitude changes could be completely reversed by the addition of nitrate at one-fourth or more of the concentration in *f/2* medium (0.88  $\mu\text{mol}$ ). The addition to autoclaved seawater of phosphate, vitamins, minerals, or soil extract in concentrations present in *f/2* medium had no effect. Thus, the shortening of the circadian period is the consequence of reduced nitrogen supply. Since both

the rhythms in bioluminescence and photosynthesis showed similarly shortened circadian periods and lower amplitudes, it is probable that the depletion of nitrate directly affects the circadian clock.

616. Sweeney, Beatrice M., David C. Fork and Kazuhiko Satoh (1982). Bioluminescence in *Gonyaulax polyedra* is Stimulated by Red Light. *Abstr., Amer. Soc. Photobiol.* 10th Ann. Meet., p. 182.

**ABSTRACT.** Bioluminescence is stimulated in *Gonyaulax polyedra* cells in scotophase by red light with a maximum effective wavelength of 670 nm. The rise time is 200 ms and the decay is logarithmic with a half-time of 1 s. The action spectrum for stimulation indicates the involvement of photosynthetically active light.

617. Sweeney, Beatrice M., David C. Fork and Kazuhiko Satoh (1983). Stimulation of Bioluminescence in Dinoflagellates by Red Light. *Photochem. Photobiol.* 37(4):457-465.

In three species of dinoflagellate, *Gonyaulax polyedra*, *Pyrocystis fusiformis* and *Pyrocystis lunula*, bioluminescence can be stimulated by light. This phenomenon is observed if the cell suspension is rendered anaerobic by any of the following treatments:  $\text{N}_2$  gas, metabolically active yeast, glucose plus glucose oxidase, dithionite, or allowing a concentrated cell suspension to stand for several hours in darkness, conditions which remove oxygen from the cell suspension. An alternate pretreatment is inclusion of carbonylcyanide-m-chlorophenyl hydrazone or hydroxylamine in the cell suspension. The emission spectrum with a maximum at 478 nm identifies dinoflagellate luciferin as the emitter. The action spectrum (maximum at 675 nm in the red region of the spectrum) points to chlorophyll as the photoreceptor. Evidence for the participation of photosystem II (PS II) of photosynthesis in the light-stimulation of bioluminescence is the strong inhibition of light emission by 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) and 2,5-dibromo-3-isopropyl-p-benzoquinone and the failure of diaminodurol + ascorbate to reverse the inhibition by DCMU. The observation that, with short irradiations (5  $\mu\text{s}$ ), no bioluminescence is emitted until the third flash also suggests PS II as the site of stimulation. The evolution of oxygen is not involved in the light-stimulation of bioluminescence, since oxygen evolution is completely inhibited by  $\text{NH}_2\text{OH}$ , while

light emission is potentiated by the presence of  $\text{NH}_2\text{OH}$ . A consideration of the action of inhibitors suggests that the stimulation of light emission is the result of a change in membrane potential produced upon irradiation of PS II. This membrane potential is not caused by the movement of protons.

618. Swift, Elijah (1982). Sources and Distributions of Oceanic Bioluminescence. Progress Report Abstracts, Office of Naval Research, December, pp. 111-112.

**ABSTRACT.** Analysis of bathyphotometer data and plankton tows from five cruises to the Sargasso Sea is completed. The data suggest that the dinoflagellate *Pyrocystis noctiluca*, copepods, larvaceans and ostracods are the major light emitters. The bioluminescence maximum layer is generally shallower than the chlorophyll maximum. Layering is pronounced in regions with high biomass. Simulated dinoflagellate flashes cause a "startled" reaction in copepods.

619. Swift, Elijah (1982). The Causes of Fire in the Sea. *Maritimes* 26(4):3-5.

The phenomenon of bioluminescence and some common luminous organisms are described. A brief history of bioluminescence research is given with specific mention of studies by the University of Rhode Island. The role of dinoflagellates as a source of light in ships' wakes is suggested to be minimal.

620. Swift, Elijah (1982). Sources and Distributions of Oceanic Bioluminescence. In ONR Oceanic Chemistry and Biology Group Program Science Report, 1 March, pp. V-37-V-38.

**ABSTRACT.** Vertical profiles of bioluminescence to depths of 200 m taken using a pump-through bathyphotometer on two cruises in the Sargasso Sea showed higher bioluminescence in the northern part than in the southern part and that the vertical bioluminescence maxima generally were not at the same depth as the chlorophyll maxima. Preliminary analysis of organisms collected at selected depths from the bathyphotometer efflux using 25  $\mu\text{m}$  nets and from net tows suggested that larvaceans and ostracods produced more than half of the observed bioluminescence.

621. Swift, Elijah (1985). Sources and Distributions of Oceanic Bioluminescence. Status Report. Annual Report to the Office of Naval Research, Vol. 1, pp. SW1-SW18.

Key organisms in producing bioluminescence have been identified as crustaceans (ostracods, copepods and euphausiids), larvaceans, colonial radiolarians and one genus of photosynthetic dinoflagellate (*Pyrocystis*) in the Sargasso and Norwegian Seas. Nonphotosynthetic dinoflagellates are important contributors to the bioluminescence field near the Polar Front. At subsurface depths the copepod *Pleuromamma abdominalis* is the most important light emitter. The light budget of various oceanic regions is heavily dependent on the biological community in each region. Thus, what is true for the Sargasso Sea may not be true elsewhere. The vertical distribution of bioluminescence shows peaks in the thermocline about 10-40 m above the deep chlorophyll maximum. These peaks are due largely to larvaceans and ostracods in the Sargasso Sea. However, at the ice edge off eastern Greenland, the chlorophyll peak, due largely to diatoms, is above the bioluminescence peak and off the east coast of Iceland both peaks are on the surface. In the North Pacific central gyre the vertical distribution, phototactic and spectral responses and response thresholds for the luminous copepod, *Pleuromamma xiphias*, are determined. Different species of *Pleuromamma* distribute themselves along different isolines during the day. No evidence for photoinhibition is found in the copepod genera *Pleuromamma* and *Lucicutia*. Freshwater zooplankton respond with a startle reaction to shadows, oceanic zooplankton to flashes and estuarine zooplankton to both.

622. Swift, Elijah, Harold Batchelder, Edward Buskey, Christopher G. Mann and Jeffrey van Keuren (1986). Estimates of the Bioluminescence at the Northern and Southern BIOWATT Stations, April, 1985. *EOS* 67(44):969.

**ABSTRACT.** Bioluminescent organisms were collected from a pumped bathyphotometer efflux using a 25  $\mu\text{m}$  mesh net and from duplicate day/night pairs of MOCNESS tows. Luminous organisms were stimulated to exhaustion in front of a shipboard photometer to estimate total light output. The contribution of each organism to the light budget was estimated from its abundance in the collections and its total light output. Distinct differences in the amount of

bioluminescence present and the types of causative organisms were found between the northern and southern Sargasso Sea.

623. Swift, Elijah, William H. Biggley and Evelyn J. Lessard (1985). Distributions of Epipelagic Bioluminescence in the Sargasso and Caribbean Seas. In *Mapping Strategies in Chemical Oceanography* (Advances in Chemistry Series No. 209), Baltimore, (Maryland): Alberto Zirino, ed., American Chemical Society, pp. 235-258.

The nature of oceanic bioluminescence and some of the problems associated with its measurement are discussed in this chapter. No present instrument accurately measures the complete bioluminescence potential of the open ocean environment. At night they measured the bioluminescence stimulated mechanically in a pump-through bathyphotometer capable of capturing weakly swimming organisms. Using this instrument, they were able to describe the bioluminescence in the upper 120 m of the northern and southern Sargasso Sea and the Caribbean Sea. In the late summer, more bioluminescent organisms and more stimulated bioluminescence were observed in the northern Sargasso Sea than in the southern part. In the fall, the station at the southern edge of the southern Sargasso Sea near the Antilles and the station in the Caribbean Sea showed the highest flashing rates (i.e., concentrations of bioluminescent organisms). The bioluminescence in the Caribbean was comparable to that in the northern Sargasso Sea. These patterns reflect some of the general oceanographic features of the Sargasso Sea.

624. Swift, Elijah, William H. Biggley, Peter G. Verity and Dale T. Brown (1983). Zooplankton Are Major Sources of Epipelagic Bioluminescence in the Southern Sargasso Sea. *Bull. Mar. Sci.* 33(4):855-863.

In the southern Sargasso Sea, they used a pump-through bathyphotometer ( $15\ 1\ min^{-1}$ ) to investigate stimuable bioluminescence of the epipelagic zone. Twenty-four percent (range 17-38%) in vertical profiles and 17% (range 6-24%) in discrete depth samples of the flashes were too bright to be produced by dinoflagellates. Of the total bioluminescence detected, these bright flashes contained in vertical profiles 60% (range 53-67%) and in discrete samples 56% (range 29-70%). There were enough bioluminescent dinoflagellates in the bathyphotometer effluent to account for less than 34%

of the total flashes detected and less than 45% of the flashes small enough to be produced by dinoflagellates. This information, combined with plankton data, suggests that bioluminescent species of copepods, larvaceans and ostracods produce more stimuable bioluminescence in the Sargasso Sea than dinoflagellates.

625. Swift, Elijah, Edward Buskey and Harold Batchelder (1986). Stimulated Bioluminescence: A Comparison of Modeled and Measured Values from Biowatt I Data. *Biowatt News* #3 (April), p. 9.

**ABSTRACT.** Bioluminescence potential estimated from 1) direct measurements of bioluminescence with a closed bathyphotometer and calculations of bathyphotometer efficiency and 2) calculated from the concentrations of bioluminescent species caught by plankton nets and shipboard measurements of their bioluminescence output when stimulated to exhaustion agree that larvaceans, copepods and ostracods are the major sources of bioluminescence during Biowatt I. In addition, the plankton tows suggest the importance of euphausiids that are not efficiently sampled by the bathyphotometer.

626. Swift, Elijah, Edward Buskey, Peter P. Neidhardt, Christopher G. Mann and J. Dugas (1985). Plankton Tows on BIOWATT I. In *Data Directory for BIOWATT I, R/V Knorr, 1-26 April 1985*, pp. 62-65.

The plankton tows taken during BIOWATT I are described along with the major experiments performed on their catches.

627. Swift, Elijah, Jeffrey van Keuren, C. Rockwell Booth and C. P. Li (1987). A Moored Instrument for Measuring Stimulated and Natural Oceanic Bioluminescence. *EOS* 68(50):1695.

**ABSTRACT.** An instrument has been designed to measure both stimulated bioluminescence and ambient bioluminescence and moored in the Sargasso Sea for a series of four-month-long deployments. A new analysis technique for estimating the intensities of natural bioluminescence from the ambient bioluminescence measurements suggests that a single light detector can be successfully used for this purpose, whereas previous instruments have used two detectors with coincidence counting circuits.

628. Swift, Elijah, Evelyn J. Lessard and William H. Biggley (1985). Organisms Associated with Stimulated Epipelagic Bioluminescence in the Sargasso Sea and the Gulf Stream. *J. Plankton Res.* 7(6):831-848.

On three cruises, vertical profiles of stimulated bioluminescence were measured during the late evening in the upper 200 m of the Sargasso Sea using a submarine photometer. On one cruise, organisms were collected in a 25  $\mu$ m porosity net after passing through the photometer where the intensity and light content of their bioluminescence were recorded. Correlations of bioluminescence and organisms suggested that the majority of the stimulated bioluminescence produced in the Sargasso Sea was from zooplankton: crustaceans (ostracods, copepods, copepod larvae, euphausiid larvae), larvaceans and colonial radiolarians. In addition, the photosynthetic dinoflagellate *Pyrocystis noctiluca* appeared to produce 5-30% of the measured bioluminescence at some stations. Other dinoflagellates, although numerous, were dim and thus produced less than a few percent of the stimulated bioluminescent light. The subsurface peaks in the Gulf Stream and northern Sargasso Sea were due primarily to ostracods and larvaceans. In the Anegada Passage in October, and in the northern Sargasso Sea and the Gulf Stream in August, there were pronounced subsurface peaks in bioluminescence associated with the thermocline. In Anegada Passage and the Sargasso Sea just north of Puerto Rico in October and in the Gulf Stream in August, the subsurface bioluminescence peak was in or slightly above the chlorophyll maximum. However, at the Sargasso Sea stations in August, it was 10-40 m above the depth of the chlorophyll maximum.

629. Swift, Elijah, John Marra, Edward Buskey, Harold Batchelder, Peter P. Neidhardt, William H. Biggley, Jeffrey van Keuren and Raymond C. Smith (1986). Factors Associated with the Vertical Distribution of Stimulated Bioluminescence in the Northern Sargasso Sea and the North Pacific Central Gyre. *Biowatt News* #6 (September), p.8.

**ABSTRACT.** North of the subtropic front in these two regions bioluminescence, due largely to copepods and larvaceans, is associated with a fluctuating chlorophyll maximum at about 50 m while productivity peaks at the surface. South of the front bioluminescence peaks 40-80 m above the chlorophyll maximum in association with the productivity peak and is due primarily to ostracods. Late summer

patterns north of the front are similar to the year-round patterns south of the front.

630. Swift, Elijah, Valerie A. Meunier, William H. Biggley, Jean Hoarau and Henri Barras (1981). Factors Affecting Bioluminescent Capacity in Oceanic Dinoflagellates. In *Bioluminescence: Current Perspectives*. Kenneth H. Nealson, ed., Minneapolis (Minnesota): Burgess Publishing Co., pp. 95-106.

In the laboratory cell volume and bioluminescence capacity of *Pyrocystis* species decrease with decreasing light intensity. Temperature and pressure changes have little effect. However, such a decrease is often not seen at sea, possibly due to vertical migration. Where nutrient-rich waters cause decreased vertical migration, there is a decrease in cell size and bioluminescence capacity with depth. More rapid losses of bioluminescence capacity may occur at depths where light intensities are below compensation levels, due to depletion from agitation by zooplankton.

631. Swift, Elijah, Peter P. Neidhardt, William H. Biggley and Raymond C. Smith (1985). Differences in Stimulated Bioluminescence: Day and Night in Epipelagic Oceanic Waters. *EOS* 66(51):1313.

**ABSTRACT.** Between day and night, stimulated bioluminescence increases by three orders of magnitude in inshore waters dominated by photosynthetic dinoflagellates, two orders of magnitude in slope waters and one order of magnitude in epipelagic oceanic waters, expressed either as rate of flashing or rate of light production. These changes apparently are due to a combination of vertical migration of the zooplankton and photoinhibition of the photosynthetic dinoflagellates.

632. Swift, Elijah, H. Rines, Peter P. Neidhardt and Edward Buskey (1983). Patterns of Epipelagic Oceanic Bioluminescence in the Norwegian Sea and the Irminger Sea, July, 1983. *EOS* 64(52):1049.

**ABSTRACT.** Surface bioluminescence in subarctic waters north of Iceland was low due to low concentrations of dinoflagellates and high ambient light. Subsurface peaks correlated with biomass subdominants, including the copepod *Metridia longa*, the euphausiid *Meganctiphanes norvegica* and the ostracod *Conchoecia borealis*. Highest bioluminescence was found in a temperature gradient of 4-9°C in the subarctic front east of Iceland. South of the subarctic front in the Irminger Sea, surface

bioluminescence was higher due to low ambient light and populations of dinoflagellate *Ceratium fusus*, while crustacean bioluminescence continued to predominate below the surface.

633. Sykes, Paul F. (1980). The Ultrastructure of the Luminescent Granules in *Oikopleura labradoriensis*. *Amer. Zool.* 20(4):850.

**ABSTRACT.** The fluorescent granules in houses of *O. labradoriensis*, from which light emission occurs, contain spherical membrane-bound microgranules bound together in an electron-dense matrix. The mucous layer contains less electron dense microgranules with a variety of shapes. Both types of microgranules contain internal membranes often in the form of myelinated annuli or tubules. The structural characteristics suggest that the microgranules may be modified mitochondria.

634. Taylor, Walter, Jay C. Dunlap and J. Woodland Hastings (1982). Inhibitors of Protein Synthesis on 80S Ribosomes Phase Shift the *Gonyaulax* Clock. *J. Exp. Biol.* 97:121-136.

One-hour pulses of anisomycin (0.3  $\mu$ M), streptimidone (30  $\mu$ M), and cycloheximide (5  $\mu$ M) caused strong phase-shifts (either advances or delays, of up to 12 hours) in the circadian rhythm of the bioluminescence glow in the marine photosynthetic dinoflagellate, *Gonyaulax polyedra*. Similar pulses of emetine (0.1-100  $\mu$ M) caused small (<4 hours) phase shifts. Drug pulses have quantitatively different effects when applied at different phases of the circadian cycle, thus giving rise to "phase response curves" (PRC's). The results lend additional support to the generalization, based on results from several different organisms, that 80S ribosome protein synthesizing system is of key importance in the mechanism responsible for circadian rhythms.

635. Taylor, Walter, Van D. Gooch and J. Woodland Hastings (1979). Period Shortening and Phase Shifting Effects of Ethanol on the *Gonyaulax* Glow Rhythm. *J. Comp. Physiol.* B130(4):355-358.

In a number of organisms which exhibit circadian rhythmicity, a continuous exposure to ethanol at moderate (0.1%) concentrations is known to cause period lengthening. In studies of the effects of ethanol on the circadian luminescence glow rhythm of the marine dinoflagellate *Gonyaulax*, we observed that 0.1% ethanol causes instead a period shortening. They

have also found that ethanol pulses cause phase shifts, with little or no after-effects on the period of the circadian rhythm which continues thereafter.

636. Taylor, Walter and J. Woodland Hastings (1979). Aldehydes Phase Shift the *Gonyaulax* Clock. *J. Comp. Physiol.* B130:359-362.

Aliphatic aldehydes ranging in chain length from one to four carbon atoms have a significant phase shifting effect upon the circadian rhythm of bioluminescence (glow) in the dinoflagellate *Gonyaulax polyedra*. Cells exposed for two hours to 18 mM acetaldehyde starting at about circadian time 12 experience a permanent phase delay of up to about 12 hours. The phase response curve relationship with acetaldehyde is presented, as well as the relationship between concentration and phase delay for the four aldehydes studied. Reactions of aldehydes which may be implicated are discussed. The possibility that sulfhydryl reagents may perturb circadian systems is suggested.

637. Taylor, Walter and J. Woodland Hastings (1982). Minute-long Pulses of Anisomycin Phase-Shift the Biological Clock in *Gonyaulax* by Hours. *Naturwissenschaften* 69:94-96.

Exposure to anisomycin, which inhibits protein synthesis on the 80S ribosome, for as little as 3-5 minutes, causes phase shifts in the circadian rhythm of bioluminescence of up to 12 hours in *Gonyaulax polyedra*. High concentrations of anisomycin exhibit phase-response curves similar to those caused by 1-hour pulses of low concentrations of anisomycin. At the lowest concentration used the phase response curve is continuous and exhibits atypical double peaking, which observation suggests that the oscillation has been driven close to its singularity, where it becomes nearly arrhythmic. The molecular mechanism by which these effects are achieved is not known, but several possible explanations are presented.

638. Taylor, Walter, Richard Krasnow, Jay C. Dunlap, Hellmuth Broda and J. Woodland Hastings (1982). Critical Pulses of Anisomycin Drive the Circadian Oscillator in *Gonyaulax* Towards Its Singularity. *J. Comp. Physiol.* B148:11-25. [Abstract published in *Abstr., Amer. Soc. Photobiol. 10th Ann. Meet.*, p. 181 (1982)].

Dose and phase response curves for phase shifting the circadian oscillator in the dinoflagellate

*Gonyaulax polyedra* were measured with pulses of the antibiotic anisomycin (an inhibitor of protein synthesis on 80S ribosomes), using the bioluminescent glow rhythm as the assay. The three dimensional surface of final phase, initial phase and concentration was found to be a right handed helix, with the axis at a critical initial phase near circadian time 12 hours and critical concentration near 0.2  $\mu\text{mol}$  anisomycin (for 1-hour pulses). The normally rhythmic glow of populations of *Gonyaulax* was significantly disrupted by pulses with these critical parameters and in many instances appeared nearly arrhythmic. With increasing drug concentration, phase-response curves appear to move bodily to earlier phases and no saturation is evident in the phase-shifting effect. These results are interpreted as indicating that anisomycin at sufficiently high doses causes an immediate strong (type 0) phase shift, then holds the clock stationary for a time interval that increases with concentration. The possibility that the 80S ribosomal complex may be centrally involved in the fundamental circadian oscillation is put forward.

639. Taylor, Walter, Steven Wilson, Robert Presswood and J. Woodland Hastings (1982). Circadian Rhythm Data Collection with the Apple II Microcomputer. *J. Interdiscipl. Cycle Res.* 13(1):71-79.

Measurement of persistent circadian rhythms of bioluminescence in the marine dinoflagellate *Gonyaulax polyedra* has been automated using the Apple II microcomputer. The mechanics of the system are under software control and allow for the measurement of up to 60 different samples for periods of at least 3 weeks, with data points for each sample every 15 minutes. Experiments are presented showing that 4-hour exposures to streptimidone, a potent inhibitor of protein synthesis on 80S ribosomes, result in phase shifts in the rhythm.

640. Tebo, Bradley M., D. Scott Linthicum and Kenneth H. Nealson (1979). Luminous Bacteria and Light-Emitting Fish: Ultrastructure of the Symbiosis. *Biosystems* 11(4):269-280.

The ultrastructure of the light organ of the Japanese Knightfish, *Monocentris japonicus*, is described in terms of its role in supporting a continuous, static culture of symbiotic luminous bacteria, *Photobacterium fischeri*. Hypotheses on the mechanism of initial infection of the light organ and metabolic integration of the fish and bacterial

symbionts are presented. Metabolic and physical mechanisms for control of light emission are described.

641. Thompson, Eric M., Basil G. Nafpaktitis and Frederick I. Tsuji (1987). Induction of Bioluminescence in the Marine Fish, *Porichthys*, by *Vargula* (Crustacean) Luciferin. Evidence for de novo Synthesis or Recycling of Luciferin. *Photochem. Photobiol.* 45(4):529-533.

The marine fish, *Porichthys notatus*, emits light by a classical luciferin-luciferase reaction whose components are similar, if not identical to those found in the luminescent crustacean, *Vargula*. *Porichthys* is divided geographically into a southern luminescent and a northern nonluminescent population. Specimens of nonluminescent *Porichthys* can be induced to become luminescent by injection or ingestion of *Vargula* luciferin. After feeding a known quantity of *Vargula* luciferin, light emitted by *Porichthys* was monitored for a 2-year period. Summation of light produced during each bioluminescence episode demonstrated that the total quanta emitted over 2 years exceeded the theoretical yield from the administered luciferin. These results indicate that the administered luciferin either recycles or induces de novo synthesis of additional luciferin in *Porichthys*.

642. Thorey, Irmgard, Isa Rode, G. Harnau and Rüdiger Hardeland (1987). Conditionality of Phase Resetting by Inhibitors of 80 S Translation in *Gonyaulax polyedra*. *J. Comp. Physiol.* B157(1):85-89.

*Gonyaulax polyedra* was subjected to a cold treatment of 18 hours at 10°C leading to arrhythmicity. Subsequently, the circadian rhythm of bioluminescence was investigated at the permissive temperature of 20°C. 1-hour pulses of 10  $\mu\text{M}$  cycloheximide or 2  $\mu\text{M}$  anisomycin, when given after the temperature step-up, resulted only in a very weak resetting of the circadian oscillator, in marked contrast to the behavior of cells kept continuously in oscillatory conditions at 20°C. The extremely reduced sensitivity to 80S inhibition was characteristic for the first cycle after the temperature step-up, whereas cells treated with cycloheximide in the second cycle after reinitiation of rhythmicity showed a gradual recovery of resetability, though the phase response curve was still atypical; treatment in the third cycle after step-up led to a relatively normal phase response curve. The

observed insensitivity in the first cycle was neither a consequence of insufficient drug action, nor of a transient nonoscillatory behavior after temperature step-up. Already in the first hours after transfer to 20°C, 80S translation was strongly suppressed by cycloheximide and the cells were also efficiently reset by changes of the light-dark zeitgeber. Resetability of the circadian oscillator by 80S inhibitors is, therefore, conditional.

643. Tokarev, Yu. N., L. A. Radchenko and V. N. Popovichev (1985). Use of Bioluminescence Characteristics for Estimating Primary Production in the Ocean. *Gidrobiol. Zh.* 21(3): 18-21. (Russian)

A correlation between bioluminescence intensity and photosynthesis is observed in waters in the euphotic zone. From 75 m to the surface correlation coefficients are high but not constant. Their variation with depth is probably due to variations in the ratio between luminous and nonluminous phytoplankton. The greatest homogeneity occurs in the topmost 25 m. This correlation offers the potential of estimating primary production accurately and quickly at night in the surface layer and of studying the three-dimensional structure of the phytoplankton community.

644. Töpperwein, F. and Rüdiger Hardeland (1980). Free-Running Circadian Rhythm of Plastid Movements in Individual Cells of *Pyrocystis lunula* (Dinophyta). *J. Interdiscipl. Cycle Res.* 11(4):325-329.

*Pyrocystis lunula*, a dinoflagellate lacking periodicity in spontaneous bioluminescence, shows a characteristic circadian rhythm of plastid movements which can be monitored photographically in individual cells. The rhythm persists under free-running conditions in constant dim light (40-50 lux), but is damped out already in LL of 100 lux.

645. Tsuji, Frederick I. (1982). Bacterial Bioluminescence: Is There a Function for the Light? In *Oxygenases and Oxygen Metabolism*, M. Nozaki, S. Yamamoto, Y. Ishimura, M. J. Coon, L. Ernster and R. W. Estabrook, eds., New York: Academic Press, pp. 239-244.

It is suggested that the theory that bacterial bioluminescence is a vestige of a primitive respiratory system may be wrong, because of the large chemical and energetic investment in the light-emitting system by the bacteria. Other functional theories are mentioned and the theory that bacterial

bioluminescence acts to deter predation upon high concentrations of luminous bacteria, much as dinoflagellate luminescence deters copepod predation, is proposed. Light-emission parameters are given.

646. Tsuji, Frederick I. (1982). Molecular Mechanisms and Function of Bioluminescence in Fishes. In *From Cyclotrons to Cytochromes: Essays in Molecular Biology and Chemistry*, Nathan O. Kaplan and Arthur Robinson, eds., New York: Academic Press, pp. 537-559.

An estimate of the prevalence of bioluminescence in deep-sea fishes is given. Fish produce luminescence in light organs either through a bacterial reaction involving symbiotic luminous bacteria or through the oxidation of luciferin catalyzed by luciferase. Both methods are used by the angler fish *Linophryne* and possibly *Himantolophus*, but other fish use only a single method. Both methods are discussed in some detail and cross-reactions with luciferins and luciferases from the ostracod crustacean *Cypridina* are noted for apogonid, pempherid, midshipman, myctophid and hatchet fishes. The question of whether these fish synthesize their own luciferin or obtain it by ingestion of *Cypridina* is discussed with respect to the midshipman fish, *Porichthys*. Various theories regarding the function of bioluminescence in fishes are presented and the countershading hypothesis receives a detailed discussion.

647. Tsuji, Frederick I. (1983). Molluscan Bioluminescence. In *The Mollusca*, Vol. 2, *Environmental Biochemistry and Physiology*, Peter W. Hochachka, ed., New York: Academic Press, pp. 257-279.

Bioluminescence is not an evenly distributed property in the Mollusca. It occurs only in 3 of the 6 taxonomic classes: Gastropoda, Bivalvia and Cephalopoda. The chemistry of bioluminescence is discussed in detail, considering symbiotic luminous bacteria in the luminous organs of squid, *Pholus dactylus*, *Latia neritoides*, *Watasenia scintillans* and *Symplectoteuthis oualaniensis*.

648. Tsuji, Frederick I. (1985). ATP-Dependent Bioluminescence in the Firefly Squid, *Watasenia scintillans*. *Proc., Nat. Acad. Sci. US* 82:4629-4632.

The Japanese firefly squid, *Watasenia scintillans*, emits intense flashes of light from three

tiny luminous organs that are located at the tip of each of a pair of ventral arms. Light is also produced from hundreds of other minute organs that are scattered over the body. The luminescence is due to an ATP-dependent reaction, with an optimal pH of 8.80. The decay of light intensity follows first-order kinetics and the decay constant is independent of initial ATP concentration. The light emission also requires  $MgCl_2$ , a soluble component and an insoluble component that is membrane bound. Squids represent a major group of organisms unrelated to fireflies in which ATP is required for bioluminescence.

649. Tsuji, Frederick I. and Elizabeth Hill (1983). Repetitive Cycles of Bioluminescence and Spawning in the Polychaete, *Odontosyllis phosphorea*. *Biol. Bull.* 165(2):444-449.

Polychaetes of the genus *Odontosyllis* from Bermuda show spawning swarms throughout the year, with lunar periodicity: shortly after sunset, the bioluminescent worms appear at the surface, where they pair and mate, for several days immediately after full moon. Similar behavior has been reported for two other species of this genus: one from Puerto Rico and another, *Odontosyllis phosphorea*, from British Columbia; lunar periodicity in the latter species, however, has been questioned. Still other species of this genus spawn only once a year. They have observed spawning swarms in *O. phosphorea* from southern California, which are similar to those described in the Caribbean, except that the spawning peaks are strongly seasonal and occur at fortnightly intervals: i.e., follow a semilunar rhythm rather than a lunar rhythm, as reported for other species of this genus.

650. Tsuji, Frederick I. and Gary B. Leisman (1981).  $K^+/Na^+$ -Triggered Bioluminescence in the Oceanic Squid *Symplectoteuthis oualaniensis*. *Proc., Nat. Acad. Sci. US* 78(11):6719-6723.

A distinctive type of luminescent system present in the large dorsal luminous organ of the oceanic squid *Symplectoteuthis oualaniensis* is described. The organ produces an intense blue flash of light followed by a rapid decay in light intensity. Luminescence originates from numerous oval granules present in the luminous organ. The essential light-emitting components are membrane bound. Intact granules or washed homogenates of the granules are triggered to emit light by monovalent cations such as, in

decreasing order of effectiveness, potassium, rubidium, sodium, cesium, ammonium and lithium. Calcium, magnesium and strontium ions do not trigger light emission. Analysis of the kinetics of the decay of light intensity suggests that two light-emitting components are involved, one decaying faster than the other. The light-emitting reaction has an absolute requirement for molecular oxygen. The optimum KCl or NaCl concentration is about 0.6 M and the optimum pH is about 7.8. A free sulfhydryl group is essential for activity.

651. Tsuji, Frederick I. and Gary B. Leisman (1982). Membrane-bound Bioluminescence in the Pelagic Squid. In *Bioluminescence in the Pacific*. I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 127-135.

The squid, *Symplectoteuthis oualaniensis*, found in the western Pacific and Indian Oceans, is self-luminous. Its light originates from numerous small photogenic granules imbedded in the connective tissue of the light organ. It does not exhibit a luciferin-luciferase reaction. Extracts emit light when injected with NaCl or KCl, but not with LiCl,  $CaCl_2$ ,  $MgCl_2$ , NADH or NADPH. Oxygen is required.

652. Turner, George K. (1985). Measurement of Light from Chemical or Biochemical Reactions. In *Bioluminescence and Chemiluminescence: Instruments and Applications*, Vol. I. Knox Van Dyke, ed., Boca Raton (Florida): CRC Press, pp. 43-78.

Spectrophotometer, fluorometer, and luminometer designs are discussed and compared. Design considerations are detailed, especially in terms of range of applicability, sensitivity, and speed. Concern is shown for sample preparation and handling and design of the sample chamber. System components, especially light detection devices, are discussed. Direct measurement and photon counting systems are described and the theoretical advantages of photon counting are analyzed. Calibration standards and techniques are described.

653. Tyul'kova, N. A. and V. S. Filimonov (1981). Photoregulation of Bioluminescence of the Heterotrophic Organism *Peridinium depressum* (Dinophyta). *Biophysics (USSR)* 26(4) :657-658 (Russian) :666-668 (English).

Bioluminescence of *Peridinium depressum* stimulated ultrasonically is depressed by light with an

intensity above  $0.3 \text{ W/m}^2$  and is restored when placed in the dark. Maximum inhibition occurs at wavelengths around 460–490 nm. The time in the dark required for restoration is directly proportional to the intensity of the exposure. Stimulation with 0.1 N acetic acid reverses the inhibition and causes prolonged glowing.

654. Uhlig, G. and G. Sahling (1982). Rhythms and Distributional Phenomena in *Noctiluca miliaris*. *Ann. Inst. Oceanog. Paris* 58(S):277–284.

Since 1963 *Noctiluca miliaris* has been cultivated in the Helgoland laboratory. Additional results of longterm field studies are based on more than 14 years continuous monitoring of the seasonal and annual distribution near Helgoland. As proved by comparative lab and field studies, cell division of *Noctiluca* follows a circadian rhythm with a maximum reproduction activity during the night. The outburst of the seasonal *Noctiluca*-bloom varies between April and June. Independently of this variation, an abrupt disintegration occurs every year precisely during the first 10 days of August. The peaks of maximum abundance always fall within the first 10 days of July, and exactly 6 months later in January, low but distinct winter peaks are apparent. It is suggested that growth of *Noctiluca* in the field follows a seasonal circannual rhythm. The distribution of *Noctiluca* in the German Bight has been studied during several summer cruises covering monthly and extended station sampling grid. Highest abundances were found off the East and North Frisian islands with a strong gradient towards the inner region of the German Bight. Consequently, *Noctiluca* shows a tidal oscillation pattern, depending on the locality of actual sampling.

655. Uhlig, G. and G. Sahling (1985). Blooming and Red Tide Phenomenon in *Noctiluca scintillans*. *Bull. Mar. Sci.* 37(2):779–780.

**ABSTRACT.** Maximum abundance of *Noctiluca scintillans* near Helgoland occurs in June and July. The maximum vertical layer is near the surface. In coastal areas near the German Bight, the maximum layer is near the bottom. These distribution patterns result from a variation in cell buoyancy attributable to the quantity of food consumed.

656. Ulitzur, Shimon and J. Woodland Hastings (1979). Control of Aldehyde Synthesis in the

Luminous Bacterium *Beneckea harveyi*. *J. Bacteriol.* 137(2):854–859.

Some of the *Beneckea harveyi* dim aldehyde mutants, all of which emit light upon addition of exogenous long-chain aldehyde, also emit light when myristic acid is added. Analysis of these myristic acid-responsive mutants indicates that they are blocked before fatty-acid formation, whereas another class of mutants, which respond only to aldehyde, appear to be defective in the enzyme(s) involved in the conversion of acid to aldehyde. Evidence is presented that this activity, designated myristic acid reductase, is coincuded with luciferase and is involved in the recycling of acid produced in the luciferase reaction, with specificity for the  $C_{14}$  compounds.

657. Ulitzur, Shimon and J. Woodland Hastings (1979). Evidence for Tetradecanal as the Natural Aldehyde and Its Turnover in Bacterial Bioluminescence. *Abstr., Ann. Meet. Amer. Soc. Microbiol.* 79:149.

**ABSTRACT.** In one class of dim aldehyde mutants of *Beneckea harveyi*, luminescence is stimulated by addition of myristic acid. When the amount of tetradecanal or myristic acid is made limiting, cyanide and other respiration-blocking agents increase light emission 60-fold. An enzyme, myristic acid reductase, which is co-induced with luciferase, appears to convert the acid to aldehyde and to be specific for the 14-carbon chain length compound.

658. Ulitzur, Shimon and J. Woodland Hastings (1979). Evidence for Tetradecanal as the Natural Aldehyde in Bacterial Bioluminescence. *Proc., Nat. Acad. Sci. US* 76(1):265–267.

Dim aldehyde mutants of the luminous bacterium *Beneckea harveyi* emit light with exogenously added long-chain aliphatic aldehyde. In one class of these mutants, luminescence is also stimulated by myristic (tetradecanoic) acid. In such mutants the amount of light obtained by the addition of a small (limiting) amount of either tetradecanal or myristic acid may be increased 60-fold by cyanide and other agents that block respiration. This indicates that the fatty-acid product of the luminescent reaction is recycled. The effect, like the stimulation by exogenous fatty acid, exhibits specificity for the 14-carbon compound, suggesting that tetradecanal is the natural aldehyde. In those aldehyde mutants that are not stimulated to emit light by fatty acids, and thus

presumably lack the recycling system, the chain-length-specific stimulation by cyanide does not occur.

659. Ulitzur, Shimon and J. Woodland Hastings (1979). Autoinduction in a Luminous Bacterium: A Confirmation of the Hypothesis. *Current Microbiol.* 2:345-348.

In some luminous bacterial species, it is postulated that luciferase is "autoinduced" by a substance produced by the bacteria themselves. This hypothesis was confirmed. In experiments with growing cultures that were subjected to repeated subculturing into or dialysis against a fresh medium, which should prevent the autoinducer from accumulating, the normal synthesis of luciferase and the development of luminescence did not occur.

660. Ulitzur, Shimon and J. Woodland Hastings (1980). Reversible Inhibition of Bacterial Bioluminescence by Long-Chain Fatty Acids. *Current Microbiol.* 3:295-300.

Long-chain unsaturated fatty acids, as well as certain saturated fatty acids such as lauric acid, are inhibitors of the in vivo luminescence of wild-type strains of four species of luminous bacteria (*Beneckea harveyi*, *Photobacterium phosphoreum*, *P. fischeri*, and *P. leiognathi*) as well as the myristic acid-stimulated luminescence in the aldehyde dim mutant M17 of *B. harveyi*. Based on studies with the system in vivo, the principal site of action of all the fatty acids appears to be the reductase activity that converts myristic acid to myristyl aldehyde. This was confirmed by in vitro studies: reductase activity in crude cell-free extracts is strongly inhibited by oleic acid.

661. Ulitzur, Shimon, A. Reinhertz and J. Woodland Hastings (1981). Factors Affecting the Cellular Expression of Bacterial Luciferase. *Arch. Microbiol.* 129:67-71.

The in vivo expression of cellular bacterial luciferase has been defined as the luciferase expression quotient, measured as the ratio of the bioluminescence intensity in vivo to the in vitro activity of luciferase in crude cell extracts. The expression is greater in the presence of inhibitors of the electron-transport system such as cyanide and N-heptyl-4-hydroxyquinoline and also at lower oxygen tensions. The higher expression of the cellular luciferase under these conditions is

postulated to be due to an increase in the intracellular levels of reduced coenzymes which enhance both the reduction of flavin and the reduction of fatty acid to aldehyde. Both FMNH<sub>2</sub> and aldehyde are substrates in the light emitting reaction.

662. Ulitzur, Shimon, M. Simaan and J. Kuhn (1987).  $\alpha$ -Subunit of Bacterial Luciferase Inhibits the Expression of the Luminescence Genes. In *Bioluminescence and Chemiluminescence: New Perspectives*, J. Schölmerich, R. Andreesen, A. Kapp, M. Ernst, and W. G. Woods, eds., New York: John Wiley and Sons, pp. 381-384. [Abstract published in *J. Bioluminescence Chemiluminescence* 1(2):139 (1986)].

The ability of *Vibrio harveyi* cells to form aldehyde or luciferase is gradually diminished shortly after induction and completely abolished at maximum luminescence. One possible explanation for this behavior is that a product of the *lux* operon is involved in a feedback control mechanism. Experiments on cloned *Escherichia coli* containing the *lux* gene suggest that control is effected at the transcription and/or translation level and is mediated probably by the  $\alpha$ -subunit of luciferase. A theory for its operation is proposed.

663. Utyushev, R. N., I. I. Gitel'zon, L. A. Levin and A. S. Artemkin (1982). Some Bioluminescent Pattern Peculiarities of Productive Regions of the Tropical Pacific. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 101-110.

A single maximum vertical distribution of bioluminescence is reported for Pacific equatorial and Peruvian coastal upwelling regions. Away from the areas of direct upwelling, stratification of bioluminescence becomes more diffuse with two and three maximum layers appearing. The distribution correlates with vertical phytoplankton distribution, with the maximum occurring at a zone of sharp decrease in prey organisms. A circadian rhythm of bioluminescence occurs, with a decrease in emission beginning to occur one to three hours, depending on depth, before an increase in astronomical downwelling light intensity.

664. Utyushev, R. N. and L. A. Levin (1982). Energetic Estimations from Bathypotometric Measurements. In *Bioluminescence in the Pacific*, I. I.

Gitel'zon and J. W. Hastings, eds., Kranoyarsk: Akad. Nauk USSR, pp. 111-122.

A bathyphotometer calibration technique based on use of stable radioluminescent light standards with emission spectra similar to that of bioluminescence is proposed. This technique has been used to determine the bioluminescence radiance flux on several expeditions.

665. Utyushev, R. N., L. A. Levin and O. A. Cherepanov (1984). Experimental Estimation of the Bioluminescence Field Structure from Daytime Measurements. *Oceanology* (USSR) 24(4):701-705 (Russian): 531-533 (English).

The intensity of the bioluminescence of individual species and their aggregates varies substantially during the day. A 5-day experiment in the northwest Pacific revealed that the nighttime intensity of the bioluminescence field exceeds the daytime intensity by one-and-one-half orders of magnitude. The quasistationary nighttime period in this region extends from 2300 to 0300, local time. The possibility of reconstructing the nighttime structure of the bioluminescence field from the measured daytime data is demonstrated.

666. Venugopalan, V. K. and A. Ramesh (1982). Luminous Microflora in the Sediments of Vellar Estuary. *Atlantica* 5(2):128

**ABSTRACT.** *Vibrio harveyi* and *V. fischeri* are identified as the major species of luminous bacteria observed in sediments in the Vellar estuary on the southeast coast of India. Fewer luminous bacteria are found in the tidal zone than either offshore or upriver beyond the tidal zone.

667. Vinogradov, M. E. (1982). The 34th Cruise of the R/V *Akademik Kurchatov*-Study of the Ecosystem of the Frontal Zone of the Southeast Pacific Ocean. *Oceanology* (USSR) 22(6):767-771 (English).

On a 4-month cruise in the southeast Pacific Ocean in 1982 the R/V *Akademik Kurchatov* performed studies of (1) the physical characteristics of frontal boundaries and zones; (2) the hydrodynamic structure of the water in frontal zones and neighboring regions; (3) the biophysical parameters of the ecosystem of the frontal zone and adjacent waters; and (4) the biocommunities and rules of their formation and growth in frontal and interfrontal water areas, and developed mathematical models of the functioning of

natural societies of the pelagic zones of the regions studied. Stations were chosen to correlate with earlier studies done in 1974, 1978, and 1980. Continuous measurements of bioluminescence intensity were made using a flow-through bathyphotometer over more than 4000 miles of the cruise track. These measurements yielded the characteristic dimensions of the horizontal inhomogeneities of the bioluminescence field and its relationship to the temperature field.

668. Vladimirov, V. L. (1979). Investigations of the Vertical Distribution of Bioluminescence in an Active Layer of Ocean. In *Optical Methods of Studying Oceans and Internal Lakes*, Novosibirsk: Izd.-Vo "Nauka," pp. 57-59.

Schools of fish, krill, and other marine organisms may be detected remotely by the bioluminescence generated by their movements, if they are in waters containing luminous plankton. An open bioluminograph that stimulates bioluminescence by the movement of its housing has been used to obtain more than 1000 vertical profiles of bioluminescence to depths of 400 m in different oceanic areas. Although this distribution undergoes diurnal changes due to light-driven vertical migrations and circadian rhythms of bioluminescence, it was found to be quasi-stationary for a 4-hour period in the middle of the night. Considerable heterogeneity was observed, with broad layers, frequently divided into smaller layers of 5-20 m in thickness, found to be correlated with the thermocline. The stability of the stratification differed in different regions, depending on the hydrodynamic conditions of the region and the species composition of the luminous organisms. In the tropical Atlantic the light field was found to be phytoplankton-dominated from the bottom of the euphotic zone (about 100-120 m) to the chlorophyll maximum (about 30-60 m) and zooplankton-dominated above the chlorophyll maximum to the surface.

669. Vladimirov, V. L., V. I. Mankov'skiy and O. V. Martynov (1981). Short-Period Fluctuations of Optical Parameters in the Photic Zone of the Ocean and Their Relationship to Fluctuations of the Thermocline. *Oceanology* (USSR) 21(5):578-581 (English).

The vertical profiles of the radiation attenuation coefficient, bioluminescence and chlorophyll fluorescence of a study area in the tropical Atlantic are

described. The relationship between the changes in these profiles and fluctuations of the thermocline is analyzed.

670. Vladimirov, V. L. and V. A. Urdenko (1979). Some Information on Bioluminescence in the Southern Ocean. *Oceanology* (USSR) 19(2):334-336 (Russian): 216-217 (English).

Brief information is given on the character of the spatial distribution of the bioluminescent field in waters of the Antarctic Circumpolar Current on a section along 20°E and also some numerical values characterizing the luminescence of the sea in the given region are presented.

671. Vladimirov, V. L. and V. A. Urdenko (1979). Correlation between Light Coefficient and Water Bioluminescence in Various Parts of the World Ocean. In *Optical Methods of Studying Oceans and Internal Lakes*, Novosibirsk: Izd-vo "Nauka," (Russian), pp. 65-68.

According to the results of measurements in the equatorial region of the Indian and Pacific Oceans, it was established that for given areas, there is a connection between the index of color and the intensity of bioluminescence. The correlation coefficients and the equations of regression between these quantities were calculated, and it was shown that the closest connection (the correlation coefficient 0.86) exists between the index of color and the total intensity of bioluminescence in the layer of 0 to 50 m.

672. Von Winckelmann, H. H. (1980). Geographic Survey of Free-Living Marine Luminescent Bacteria of the Hyponeuston. *Amer. Zool.* 20 (4):850.

**ABSTRACT.** 939 strains of luminous bacteria, all *Photobacterium fischeri*, were isolated from the upper cm of sea water at five locations along the Pacific coast of Mexico and southern California, in March, 1980. A statistical analysis indicates the possibility of an ecological province.

673. Vorob'eva, T. I., V. V. Zavoruev, V. V. Mezhevikin and G. A. Primakova (1982). Kinetic Properties of Luciferase and Taxonomy of Luminescent Bacteria. *Microbiology* (USSR) 51(3):420-423 (Russian):346-350 (English).

A comparative analysis was performed of the kinetic properties of bacterial luciferases from different species of luminescent bacteria. Considerable

species-related differences in the kinetics of the luminescent reaction were noted when myristic-, lauric-, and decyl-aldehydes were used as luciferase substrates. This permits a rapid evaluation of the species composition of a large number of luminescent bacterial strains.

674. Vysotskii, Ye. S., E. K. Rodicheva, and G. Ya. Shcherbakova (1981). The Quantum Yield of Bacterial Luminescence. *Microbiology* (USSR) 50(4):581-584 (Russian):419-421 (English).

The lower limit of the quantum yield of the bioluminescence reaction in vivo with respect to oxygen was estimated. A calculation of the fraction of oxygen used for luminescence, performed with consideration of the stoichiometry of the reaction in vitro under the condition that all the oxygen is consumed for bioluminescence at the moment of maximum luminescence, showed that the quantum yield of the reaction in the case is no less than 0.5.

675. Vysotsky, E. S., V. V. Zavoruev, G. S. Kalacheva and V. V. Mezhevikin (1982). Investigation of Aldehyde Factor From the Luminous Bacterium *Photobacterium leiognathi*. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Akad. Nauk USSR, Krasnoyarsk, pp. 314-323.

Lipids extracted from *Photobacterium leiognathi* strain 262 by chloroform/methanol and thin-layer chromatography after brief lysis were studied for their activity as substrates of bacterial luciferase. The active "aldehyde factor" was found to be close to lauric aldehyde, but not identical to it or to myristic or decyl aldehyde.

676. Vysotskii, E. S., V. V. Zavoruev and V. V. Mezhevikin (1981). Influence of Phenobarbital on Luminescent System of Luminous Bacteria. *Microbiology* (USSR) 50(6):985-991 (Russian):735-740 (English).

The effect of phenobarbital on the luminescent system of the luminous bacteria *Benickea harveyi* was investigated. It was established that the inhibition of luminescence by phenobarbital is due to a disturbance in the synthesis of an aldehyde factor, the endogenous substrate of bacterial luciferase. After treatment with phenobarbital the bacteria acquire the properties of aldehyde mutants, i.e., their luminescence is stimulated by exogenous decyl aldehyde. An investigation of the stimulation of luminescence in the culture investigated

by long-chain aldehydes, fatty acids, and their analogs suggested that the aldehyde factor is formed through the incorporation of an oxygen atom into the terminal methyl group of the saturated fatty acid or its analog. Phenobarbital does not affect the growth of luminous bacteria, however, it increases the content of luciferase in the culture. It can be assumed from the data obtained that phenobarbital is not a direct inducer of luciferase synthesis. The stimulatory effect of phenobarbital may be due to inhibition of the synthesis of the aldehyde factor and, consequently, to an increase in the concentration of intermediate products of its synthesis.

677. Vysotskii, E. S., V. V. Zavoruev and V. V. Mezhevikin (1981). Mechanism of Inactivation of Luminescent System of *Photobacterium mandapamensis*. *Microbiology (USSR)* 50(3):410-413 (Russian):275-278 (English).

It was found that in the luminescent bacterium *Photobacterium mandapamensis* (*leiognathi*), strain 54, in contrast to the other species studied, the luminescence intensity in vitro, which characterizes the luciferase activity, also decreases in the phase of luminescence attenuation. The decrease in the luminescence intensity in extracts of disintegrated bacteria is due to the loss of activity of the enzyme itself. Rifampicin and chloramphenicol prevent the drop in luciferase activity in this phase. The results obtained suggest that this strain has a special mechanism for inactivation of the luminescent system.

678. Vysotskii, E. S., V. V. Zavoruev and V. V. Mezhevikin (1981). Mechanism of Synthesis of Aldehyde Factor in Luminescent Bacteria. *Dokl. Biophysics* 256(4):995-998 (Russian):34-36 (English).

Phenobarbital inhibits, but does not completely quench, light emission from *Beneckeia harveyi*. The inhibition is partially reversed by addition of exogenous aliphatic aldehyde. Phenobarbital does not act directly on luciferase, but on the synthesis of an "aldehyde factor" that differs from decanal but appears to be related to 14-carbon aldehydes. It is postulated that the aldehyde factor is an aldehyde acid.

679. Vysotskii, E. S., V. V. Zavoruev and V. V. Mezhevikin (1982). NADPH- and ATP-Dependent Luminescence of Extracts of Luminescent Bacteria.

*Biochemistry (USSR)* 47(12):1983-1987 (Russian):1682-1686 (English).

It was found that extracts can be obtained from luminescent bacteria, whose luminescence is stimulated by the addition only of NADPH and ATP, neither the FMN nor the long-chain aliphatic aldehydes usually used for exciting the luminescence of extracts of luminescent bacteria in vivo being required for this. An aldehyde factor, a natural analog of aliphatic aldehydes, is synthesized in these extracts. The enzymatic system used for maintaining the luminescence of NADPH and ATP is probably not involved in the functioning of NAD(P)H:FMN oxidoreductase, whose involvement in luminescent processes in vivo was postulated until now. It can be assumed that both the synthesis of the aldehyde factor and the reduction of the endogenous analog of FMN, natural substrates of bacterial luciferase, are due to the functioning of the same metabolic pathway.

680. Vysotskii, E. S., V. V. Zavoruev, V. V. Mezhevikin, E. K. Rodicheva, A. M. Fish and I. I. Gitel'zon (1981). Bioluminescence of Cell-Free Extracts of Luminous Bacteria. *Dokl. Akad. Nauk USSR Ser. Biophys.* 261(1):216-219 (Russian):185-188 (English).

In contrast to the bright bioluminescence of intact luminous bacterial cells, cell-free extracts of luminous bacteria exhibit only dim luminescence without addition of exogenous substances. A method of rapidly disintegrating and extracting bacterial cells to preserve a high level of natural luminescence is presented. It is established that in the natural state a complex of at least two easily separable enzymes is involved in light production, and that the aldehyde factor (probably lauric aldehyde or a nearly identical analog) is tightly bound to the luciferase.

681. Wall, Lee C., David M. Byers and Edward A. Meighen (1984). In Vivo and In Vitro Acylation of Polypeptides in *Vibrio harveyi*: Identification of Proteins Involved in Aldehyde Production for Bioluminescence. *J. Bacteriol.* 159(2):720-724.

Incubation of soluble extracts from *Vibrio harveyi* with [<sup>3</sup>H]tetra-decanoic acid (+ATP) resulted in acylation of several polypeptides, including proteins with molecular masses near 20 kilodaltons (kDa), and at least five polypeptides in the 30- to 60-kDa range. However, in growing cells pulse-labeled in vivo with

[<sup>3</sup>H]tetradecanoic acid, only three of these polypeptides, with apparent molecular masses of 54, 42, and 32 kDa, were specifically labeled. When extracts were acylated with [<sup>3</sup>H]tetradecanoyl coenzyme A, on the other hand, only the 32-kDa polypeptide was labeled. When luciferase-containing dark mutants of *V. harveyi* were investigated, acylated 32-kDa polypeptide was not detected in a fatty acid-stimulated mutant, whereas the 42-kDa polypeptide appeared to be lacking in a mutant defective in aldehyde synthesis. Acylation of both of these polypeptides also increased specifically during induction of bioluminescence in *V. harveyi*. These results suggest that the role of the 32-kDa polypeptide is to supply free fatty acids, whereas the 42-kDa protein may be responsible for activation of fatty acids for their subsequent reduction to form the aldehyde substrates of the bioluminescent reaction.

682. Wall, Lee A., Angel Rodriguez and Edward A. Meighen (1984). Differential Acylation In Vitro with Tetradecanoyl Coenzyme A and Tetradecanoic Acid (+ATP) of Three Polypeptides Shown to Have Induced Synthesis in *Photobacterium phosphoreum*. *J. Biol. Chem.* 259(3):1409-1414.

Acylation of extracts of *Photobacterium phosphoreum* at different stages of growth with [<sup>3</sup>H]tetradecanoic acid (+ATP) has shown that two polypeptides found in the fatty-acid reductase complex, the fatty acid activating enzyme (50K) and the 34K polypeptide, were specifically labeled during induction of the luminescent system. An alternate method for in vitro acylation of polypeptides in the luminescent system was developed using tetradecanoyl-CoA. Both the 34K polypeptide and, to a lesser extent, the acyl-CoA reductase component (58K) in the complex, were acylated with [<sup>3</sup>H]tetradecanoyl-CoA. In contrast, the fatty acid activating enzyme (50K) was not labeled. Labeling of both the 34K and 58K polypeptides with [<sup>3</sup>H]tetradecanoyl-CoA as well as the acyl-CoA reductase activity in extracts paralleled the induction of luciferase during growth. Differential labeling of *P. phosphoreum* cells with [<sup>35</sup>S]methionine before luminescence induction and with [<sup>3</sup>H]methionine after the onset of luminescence followed by purification of luciferase and the polypeptides in the fatty-acid reductase complex demonstrated that the  $\alpha$  and  $\beta$  subunits of luciferase and the 34K, 50K, and 58K polypeptides of the complex had <sup>3</sup>H/<sup>35</sup>S ratios at least

7-fold higher than the constitutive proteins. These results give evidence that the synthesis of the component polypeptides of the fatty-acid reductase are induced during the development of bioluminescence and may be under the same control as luciferase. The experiments also showed that *P. phosphoreum* may have the highest content of luciferase of any luminescent bacterium, constituting approximately 20% of the total soluble protein in extracts.

683. Wall, Lee A., Angel Rodriguez and Edward A. Meighen (1986). Intersubunit Transfer of Fatty Acyl Groups during Fatty Acid Reduction. *J. Biol. Chem.* 261(34):15,981-15,988.

Fatty acid reduction in *Photobacterium phosphoreum* is catalyzed in a coupled reaction by two enzymes: acyl-protein synthetase, which activates fatty acids (+ATP), and a reductase, which reduces activated fatty acids (+NADPH) to aldehyde. Although the synthetase and reductase can be acylated with fatty acid (+ATP) and acyl-CoA, respectively, evidence for acyl transfer between these proteins has not yet been obtained. Experimental conditions have now been developed to increase significantly (5-30-fold) the level of protein acylation so that 0.4-0.8 mol of fatty-acyl groups are incorporated per mole of the synthetase or reductase subunit. The acylated reductase polypeptide migrated faster on sodium dodecyl sulfate-polyacrylamide gel electrophoresis than the unlabeled polypeptide, with a direct 1 to 1 correspondence between the moles of acyl group incorporated and the moles of polypeptide migrating at this new position. The presence of 2-mercaptoethanol or NADPH, but not NADP, substantially decreased labeling of the reductase enzyme, and kinetic studies demonstrated that the rate of covalent incorporation of the acyl group was 3 to 5 times slower than its subsequent reduction with NADPH to aldehyde. When mixtures of the synthetase and reductase polypeptides were incubated with [<sup>3</sup>H]tetradecanoic acid (+ATP) or [<sup>3</sup>H]tetradecanoyl-CoA, both polypeptides were acylated to high levels, with the labeling again being decreased by 2-mercaptoethanol or NADPH. These results have demonstrated that acylation of the reductase represents an intermediate and rate-limiting step in fatty-acid reduction. Moreover, the activated acyl groups are transferred in a reversible reaction between the synthetase and reductase proteins in the enzyme mechanism.

684. Wall, Lee A., Angel Rodriguez, Rose Szittner and Edward A. Meighen (1987). Mechanism of Fatty Acid Activation and Reduction to Form Long Chain Aldehydes for Bacterial Bioluminescence. In *Bioluminescence and Chemiluminescence: New Perspectives*, J. Schölerich, R. Andreesen, A. Kapp, M. Ernst, and W. G. Woods, eds., New York: John Wiley and Sons, pp. 401-404, (Abstract published in *J. Bioluminescence Chemiluminescence* 1(2):140, 1986).

In *Photobacterium phosphoreum* long-chain aldehyde biosynthesis is catalyzed by an enzyme complex consisting of an ATP-dependent synthetase which activates free fatty acids, an NADPH-dependent reductase which reduces them to aldehydes, and a transferase which assists in the supply of free fatty acids. The acyl-synthetase intermediate formed in the first step will turn over only in the presence of the reductase, and either the reductase or the transferase must be present to achieve a high degree of acylation. The fatty-acid reduction involves the reversible transfer of an activated acyl group between the synthetase and the reductase. A reaction mechanism is shown.

685. Walz, Brigitte and Beatrice M. Sweeney (1979). Cycloheximide Affects Two Sites of the Circadian Clock in *Gonyaulax polyedra*. *Abstr., Amer. Soc. Photobiol. 7th Ann. Meet.*, p. 68.

**ABSTRACT.** Strong concentrations of cycloheximide affect two sites of the *Gonyaulax* circadian clock, one reached after 15 min, the other after 2 hours. Weak concentrations affect only the first site. Strong pulses cause phase shifts similar to light pulses in constant darkness. Weak pulses cause phase shifts similar to "membrane active" compounds, which fact suggests that the first site is closely related to membranes.

686. Walz, Brigitte and Beatrice M. Sweeney (1979). Kinetics of the Cycloheximide Phase Changes in the Biological Clock in *Gonyaulax*. *Proc., Nat. Acad. Sci. US* 76(12):6443-6447.

Cycloheximide, an inhibitor of protein synthesis on cytoplasmic ribosomes in eukaryotes, is shown to shift the phase of the circadian rhythm in stimulated bioluminescence in the marine dinoflagellate *Gonyaulax polyedra*. Kinetic analysis of the phase changes shows that the effect may be subdivided into two distinctly different and well-separated parts. The

first (early) phase change occurs with 15-min exposure to cycloheximide and is saturated at low concentrations (about 10 nM). The second (late) phase change requires about 150 min of exposure to cycloheximide and is saturated at 0.36  $\mu$ M cycloheximide. Twenty-times-higher concentrations cause no further phase changes. The magnitudes of both early and late phase changes depend on the time of day when the cells are exposed to cycloheximide. Early phase changes vary from 5 hr advance at circadian time, (CT) 20 to 1 hour delay at CT 12; late phase changes are larger, the maximal advance being 12 hours at CT 16 and the greatest delay, 10 hours at CT 14. It is proposed that the early phase changes are caused by alteration in the ion distribution across membranes as a consequence of the permeation of cycloheximide. Late phase changes may be the result of inhibition of protein synthesis. The phase-reponse curve for the late phase change is identical to that obtained with saturating light pulses in otherwise constant darkness in *Gonyaulax*. Maximal phase changes drive the clock into the part of the circadian cycle between CTs 4 and 9. Perturbations in this part of the circadian cycle are without effect on phase. Incubation of *Gonyaulax* with cycloheximide for a critical duration at a critical time induces arrhythmicity, but longer exposures to the inhibitor at the same time do not. This observation suggests the existence of a singularity in the circadian clock of *Gonyaulax*.

687. Walz, Brigitte, Alfred Walz and Beatrice M. Sweeney (1983). A Circadian Rhythm in RNA in the Dinoflagellate, *Gonyaulax polyedra*. *J. Comp. Physiol.* B151(2):207-213.

The total RNA in stationary-phase cultures of the dinoflagellate, *Gonyaulax polyedra*, in continuous light showed a well-defined circadian rhythm, as measured by the fluorescence of cells stained with acridine orange. The maximum RNA was found at CT 18 and was followed by a sharp drop in RNA content. The rhythm in RNA content could be phase-shifted by light in the same way as the rhythm in bioluminescence. Ribosomal RNA synthesis, as measured by the incorporation of  $^{32}$ P into extracted RNA, was also rhythmic. New RNAs appeared at CT 18, as shown by acrylamide/agarose gel electrophoresis. Three to four hours later these RNAs had disappeared. These findings suggest a role of transcription in the expression of circadian rhythmicity in *Gonyaulax*.

688. Wampler, John E. (1978). Measurements and Physical Characteristics of Luminescence. In *Bioluminescence in Action*, Peter J. Herring, ed., New York: Academic Press, pp. 1-48.

The nature of light and units of its measurement are discussed. The spectra, kinetics, and yield of bioluminescence reactions and the excited states of the chemical components are analyzed. Environmental effects that can alter these characteristics are considered. Techniques and instruments for measuring spectra and light yields (relative and absolute) are described. Data analysis techniques are mentioned.

689. Wampler, John E. (1981). Calibration and Optimization of Instrumentation for Low-Level Bioluminescence Measurements. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis, (Minnesota): Burgess Publishing Co., pp. 12-28.

The physics of light measurement is discussed, with emphasis on scattering, absorption, trapping, reflection, refraction, distance attenuation, and point spread. Radiometric, spectrographic, and spectrophotometric instruments are considered both theoretically and practically for their capability to improve sensitivity, speed, accuracy, and SNR. Numerical conversion, signal processing techniques and calibration are discussed. Examples of applications are provided.

690. Wampler, John E. (1981). Earthworm Bioluminescence. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 249-256.

Luminescence in oligochaetes originates in a viscous fluid exuded by the worms from the coelomic cavity following stimulation. In many species it is associated with large cells suspended in the fluid, but this association is questionable in *Pontodrilus bermudensis*, *P. matsushimensis*, and *Microscoclex phosphoreum*, which also lack dorsal pores through which other worms exude the luminescent fluid. Luminescence is due to a luciferin-luciferase reaction stimulated by  $H_2O_2$  and not requiring oxygen. A table of spectra is given. Cross-reactions among worm species suggests similar biochemistry throughout the oligochaetes.

691. Wampler, John E. (1983). Demonstration of a Cellular Source of Bioluminescence in *Pontodrilus bermudensis*. *Photochem. Photobiol.* 37(Suppl.):S71.

**ABSTRACT.** Small coelomic cells identified as mucocytes in the luminescent fluid of the marine littoral earthworm, *Pontodrilus bermudensis*, contain numerous granular particles and exhibit a fluorescence spectrum similar to the in vivo bioluminescence spectrum ( $\lambda_{max} = 550$  nm). Using low-light-level video microscopy these cells can be identified as the source of the bioluminescence.

692. Wampler, John E. (1984). Analog and Digital Methods for Enhancing Quantum Limited Images. *Photochem. Photobiol.* 39(Suppl.):76S.

**ABSTRACT.** A computerized low-light video microscope system can enhance quantum-limited images, such as are seen in many bioluminescence studies, by averaging images and processing digital images. By also using a SIT vidicon with a reduced-intensity scanning electron beam coupled to a high-gain image intensifier, image lag may be induced to give an analog, but low-contrast, form of image averaging. Video slicing may then be used to enhance contrast and exclude low-intensity non-photon noise, to yield a final image comparable to those of standard computer enhancements.

693. Wampler, John E. (1985). Enhancing Real-Time Perception of Quantum Limited Images from a Doubly Intensified SIT Camera System. *Computer Vision Graphics Image Processing* 32:208-220.

By a combination of three enhancing procedures, the visual perception of quantum-limited images from a sensitive low-light camera system has been improved with significantly less image lag than is obtained using digital averaging alone. The camera system employed consists of a dual microchannel plate-image intensifier optically coupled to a silicon-intensified target vidicon. With this camera system a major portion of the background noise can be removed by passing the video signal through an adjustable video-slice circuit which excludes low-level signals and represents signals above the slice threshold with a uniform white value. In addition, real-image information can be integrated on the vidicon target by reducing the vidicon-beam current to induce image lag of up to 2 sec duration. Finally, the remaining noise which is characterized by lack of lag can be easily removed by

moderate digital averaging. The enhancement obtained by these techniques is continuously variable allowing the user to select an enhancement level appropriate for the image under study.

694. Wampler, John E. (1985). Instrumentation: Seeing the Light and Measuring It. In *Chemi- and Bioluminescence*, J. Burr, ed., New York: Marcel Dekker, Inc., pp. 1-44.

The nomenclature of optical measurements, including units of measurement, are defined. Detector types and their characteristics are discussed in relation to the nature of the source and signal. Radiometry and spectrometry are discussed in detail. Calibration is emphasized in both discussions.

695. Wampler, John E. (1985). Low-Light Video Systems. In *Bioluminescence and Chemiluminescence: Instruments and Applications*, Vol. II. Knox Van Dyke, ed., Boca Taton (Florida): CRC Press, pp. 123-145.

Video-camera tubes and solid state devices for low-light detection are described and performance criteria established. Intensified systems are discussed as well as the practicality of some available instrumentation for field work. Recording equipment is discussed. The limitations and advantages of digitization are considered and digitizers, frame storage, and image processing techniques are mentioned.

696. Wampler, John E. (1986). Microspectrofluorometry with an Intensified Vidicon Detector and Whole Image Spectral Scanning. In *Applications of Fluorescence in the Biomedical Sciences*, D. L. Taylor et al., eds., New York: Alan R. Liss, Inc., pp. 301-319.

An imaging system consisting of a single-photon-counting video camera coupled to a digitizer, interference filter, and computer processor is described. Both the hardware components and software are discussed. The system is applied to measuring fluorescence spectra and intensity of a moss cell and fluorescing solutions and the results analyzed. Applications to bioluminescence are possible.

697. Wampler, John E. (1986). Quantitative Low-Light Video Microscopy for Luminescence Analysis. *Photochem. Photobiol.* 43 (Suppl.):40S.

**ABSTRACT.** Computerization of low-light video microscope detectors allows for spatially resolved, quantitative measurements over the entire image field. Temporal and spatial changes can be visualized in real-time. Addition of an image quality monochromator to the viewing axis allows attainment of spectral resolution. Digital averaging can reduce noise (at the expense of temporal resolution) and non-linearity, image aliasing and spatial response variations can be overcome by proper calibration, correction and operating procedures. SNR ratios less than 1 can be visualized. Image quality graded spectrum interference filters can be used for spectral measurements over the whole image field.

698. Wampler, John E. and John C. Gilbert (1985). The Design of Custom Radiometers. In *Bioluminescence and Chemiluminescence: Instruments and Applications*, Vol. I. Knox Van Dyke, ed., Boca Raton, (Florida): CRC Press, pp. 129-150.

Theoretical and practical considerations in designing radiometers for special purposes are discussed. Instruments presently in use are analyzed and compared.

699. Wampler, John E. and Barrie G. M. Jamieson (1986). Cell Bound Bioluminescence from *Pontodrilus bermudensis* and Its Similarities to Other Earthworm Bioluminescence. *Comp. Biochem. Physiol.* 84A(1):81-87.

*Pontodrilus bermudensis* (Acanthodrilidae: Oligochaeta) is a small, bioluminescent, marine littoral earthworm species. When properly isolated, the luminescence system is contained within (14.4  $\mu$ m mean diameter) granule-filled coelomic cells. These cells were previously characterized as mucocytes. The bioluminescence of these cells can be stimulated by agitation, by addition of hypotonic hydrogen peroxide and by addition of hypotonic synthetic earthworm luciferin, but hypotonicity alone stimulates little luminescence. The spectrum of the bioluminescence ( $\lambda_{max} = 540$  nm) matches the fluorescence spectrum of the cells and a one-to-one correlation exists between bioluminescent and fluorescent cells. The data suggest that luciferin activity in *P. bermudensis* is packaged in a subcellular organelle. Comparison with other bioluminescent earthworm species shows that the bioluminescent system of *P. bermudensis* is very similar to the others studied to date.

700. Ward, William W. (1979). Energy Transfer Processes in Bioluminescence. *Photochem. Photobiol. Rev.* 4:1-57.

A comprehensive review of bioluminescence systems in general, covering biochemistry, biophysics, reaction mechanisms, excitation mechanisms, cellular organization, and other topics is provided. Emphasis is placed on energy transfer reactions, with detailed discussions of the coelenterate, bacterial, *Latia*, fungal and euphausiid systems.

701. Ward, William W. (1981). Bioluminescence: Biochemical and Physiological Advances. *Photochem. Photobiol.* 33:965-974.

Progress in studies of the physiology and biochemistry of bioluminescence since 1979 is reviewed. Bacterial studies concentrate on the nature of the emitting intermediate, autoinduction, regulation of emission, reaction energetics, the involvement of tetradecanal and myristic acid, and energy transfers to lumazine proteins resulting in spectral emission shifts. Additional coelenterate lumazine proteins resulting in spectral emission shifts. Additional coelenterate photoproteins have been characterized and their spectral emission determined. Spectral shifts involving green-fluorescent proteins also have been determined. A cross-reaction between dinoflagellate luciferin and euphausiid photoprotein is discussed. A new bioluminescence system found in squids is mentioned.

702. Ward, William W. (1985). General Aspects of Bioluminescence. In *Chemi- and Bioluminescence*, John G. Burr, ed., New York: Marcel Dekker, Inc., pp. 321-358.

A brief historical introduction to bioluminescence research is given. The evolution of bioluminescence and phylogenetic relationships among luminous organisms are elegantly discussed in great detail. Ecological functions and mechanisms for light emission in many organisms are presented. Promising areas for highly productive focused future research are suggested.

703. Ward, William W. and Milton J. Cormier (1979). An Energy Transfer Protein in Coelenterate Bioluminescence. Characterization of the *Renilla* Green-Fluorescent Protein. *J. Biol. Chem.* 254(3):781-788.

Bioluminescence in the sea pansy, *Renilla reniformis*, a marine anthozoan coelenterate, is a

complex process involving the participation of three proteins: (1) the luciferin-binding protein, (2) the enzyme luciferase, and (3) the green-fluorescent protein (GFP). Luciferin-binding protein is a specific substrate-binding protein which binds one molecule of coelenterate-type luciferin per molecule of protein and which then "releases" luciferin in the presence of  $\text{Ca}^{2+}$ . Luciferase is the enzyme which catalyzes oxidation (by  $\text{O}_2$ ) of coelenterate-type luciferin, leading to the production of  $\text{CO}_2$  and enzyme-bound excited-state oxyluciferin. Oxyluciferin may then emit blue light by a direct de-excitation pathway or may transfer excitation energy to GFP. GFP is a noncatalytic accessory protein which accepts excitation energy from oxyluciferin, by radiationless energy transfer, and then emits green bioluminescence. In this paper the purification methods and physico-chemical characteristics of GFP from *R. reniformis* are presented. GFP was purified 12,000-fold to homogeneity from crude extracts of *R. reniformis* and characterized as a dimer of identical subunits held together by noncovalent forces. A monomer molecular weight of 27,000 was determined. GFP has an intense absorption band with a maximum at nm and a molar extinction coefficient for the dimer of 270,000. The emission spectrum, which peaks at 509 nm, is a mirror image of the absorption (excitation) spectrum. Its fluorescence quantum yield of 80% results from the presence of a covalently bound chromophore of unknown chemical structure. The addition of GFP (at  $5 \times 10^{-7}$  M) to an in vitro system containing luciferin and luciferase produces a shift in the spectral distribution of light emission from blue to green and increases the radiative quantum yield by a factor of 3.1. This in vitro energy-transfer process is mediated by specific protein-protein interaction between luciferase and GFP. The *Renilla* bioluminescence system is thus the first radiationless energy transfer system the individual components of which have been purified to homogeneity, characterized, and then reassembled in vitro with restoration of the energy-transfer function.

704. Warner, Jon A. (1979). Bioluminescence in the Fish *Porichthys notatus*: Is it Based on the Occurrence of a Sympatric Luminescent Ostracod? *Abstr., Western Soc. Naturalists 60th Ann. Meet.* 60:41.

**ABSTRACT.** A naturally nonluminous variety of the fish *Porichthys notatus* is found in the Puget Sound area, separated by a gap of 1,100 km from a

naturally luminous population of the same fish off southern California. The presence of luminescence in the southern population is correlated with the presence of the luminous ostracod crustacean *Vargula tsujii*. Feeding this ostracod to nonluminous *Porichthys* of the northern population induces luminescence indistinguishable upon stimulation from that of the naturally luminous southern population.

705. Warner, Jon A. (1980). Bioluminescence in Some Marine Organisms. Ph.D. Dissertation, University of California, Santa Barbara.

The mesopelagic shrimp *Sergestes similis* matches its bioluminescence directionally, spectrally, and in intensity to downwelling background light intensity. The photoreceptors are its eyes or adjacent tissue. The myctophid fish *Symbolophorus californiensis* behaves similarly, but precedes its countershading behavior with a quick flash, similar to a startle response. The midshipman fish, *Porichthys notatus*, is luminous only where its range overlaps that of the luminous ostracod crustacean *Vargula tsujii*. Luminescence may be induced in nonluminous *Porichthys* by feeding on *Vargula*.

706. Warner, Jon A. (1981). Zooplankton Bioluminescence: *Sergestes similis*. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed. Minneapolis, (Minnesota): Burgess Publishing Co., pp. 139-142.

The decapod shrimp *Sergestes similis* countershades, matching downwelling light in intensity, spectrum and direction within an intensity range of  $6 \times 10^{-6} \mu\text{W}/\text{cm}^2$  to  $10^{-4} \mu\text{W}/\text{cm}^2$  and migrates vertically at dawn and dusk along an isolume of  $10^{-5}$  to  $10^{-6} \mu\text{W}/\text{cm}^2$ .

707. Warner, Jon A., A. Charles Arneson, Roswell W. Austin, Douglas Bailey, George Huszar, Peter James, Ronald R. McConnaughey, Kenneth H. Nealson and Edwin A. Stephan (1984). Scripps Canyon Sea Structure: A Design and Deployment for the Study of Oceanic Bioluminescence. *Mar. Tech. Soc. J.* 17(4):40-47.

A bathyphotometer for continuously measuring bioluminescence over a long period of time has been designed, built and moored in Scripps Canyon about a mile from Scripps pier. Details of the design, data acquisition and storage systems and mooring are presented.

708. Warner, Jon A. and James F. Case (1980). Cryptic Bioluminescence: Its Measurement and Imaging in Marine Organisms. *Amer. Zool.* 20(4):850.

**ABSTRACT.** The hypothesis that downwelling bioluminescence in marine organisms serves the cryptic purpose of countershading to avoid predation is expressed and supported by experimental evidence and film behavioral records.

709. Warner, Jon A. and James F. Case (1980). The Zoogeography and Dietary Induction of Bioluminescence in the Midshipman Fish, *Porichthys notatus*. *Biol. Bull.* 159(1):231-246.

*Porichthys notatus* occurs in coastal waters from Baja California to southeastern Alaska. Its light-producing system cross-reacts with that of *Vargula* (*Cypridina*) *hilgendorffii*. In the southern part of its range it is contiguous with *Vargula tsujii*, closely related to *V. hilgendorffii*. The population of *P. notatus* in Puget Sound is not bioluminescent, even though it appears to be identical to *P. notatus* from elsewhere. *V. tsujii* does not live in Puget Sound. *P. notatus* specimens from southern California contain luciferin throughout their bodies, but luciferin is lacking in the Puget Sound population. Injection of luciferin from *V. hilgendorffii* or feeding on dried *V. hilgendorffii* induces luminescence in Puget Sound *Porichthys*. Oxidized *V. hilgendorffii* luciferin and luciferin analogs do not induce luminescence, nor do luciferins from other luminous organisms. Induced luminescence lasts for months. The distribution of luminous and nonluminous *Porichthys* corresponds exactly with the presence or absence of *V. tsujii*, on which *Porichthys* in its range is known to feed. These observations suggest a dietary dependency of *P. notatus* on *V. tsujii* for luciferin.

710. Warner, Jon A., Michael I. Latz and James F. Case (1979). Cryptic Bioluminescence in a Midwater Shrimp. *Science* 203:1109-1110.

The mesopelagic shrimp *Sergestes similis* emits ventrally directed bioluminescence that closely matches the intensity of downward-directed illumination and is able to rapidly modify its light output to match changes in background intensity. Masking experiments show that the photoreceptors involved are the compound eyes or adjacent tissues. Light emission originates from modified portions of the hepatopancreas and is similar to oceanic light in angular distribution and spectral characteristics.

Normally oriented animals respond minimally to upward-directed light.

711. Watanabe, Haruo and J. Woodland Hastings (1986). Expression of Luminescence in *Photobacterium phosphoreum*: Na<sup>+</sup> Regulation of In Vivo Luminescence Appearance. *Arch. Microbiol.* 145:342-346.

In *Photobacterium phosphoreum* strain 496, growth and luminescence in a complex medium are optimal with 3% NaCl. However, in the same medium with 1% NaCl growth is similar, but the development of bioluminescence does not occur. In cells grown to mid- or late-log phase in 1% NaCl, light emission can be triggered by the addition of NaCl, but the time required for its appearance is quite long, at least 30-45 min. The synthesis of m-RNA and protein are required for the development of luminescence, but the long time interval suggests that some intermediate steps are required. The time required is not less in conditioned 3% NaCl medium.

712. Watanabe, Haruo and J. Woodland Hastings (1987). Enhancement of Light Emission in the Bacterial Luciferase Reaction by H<sub>2</sub>O<sub>2</sub>. *J. Biochem.* 101:279-282.

In the bacterial luciferase reaction, light emission is due to the mixed function oxidation of FMNH<sub>2</sub> and long chain aldehydes, which leads to the formation of an electronically excited product species, postulated to be luciferase-bound 4a-hydroxy flavin. In the present work it was found that H<sub>2</sub>O<sub>2</sub> stimulates an additional and kinetically distinct luminescence. The stimulation is more apparent in reactions inhibited by long chain alcohols and the H<sub>2</sub>O<sub>2</sub> is effective even if added secondarily. The stimulation requires H<sub>2</sub>O<sub>2</sub> only at the outset; its subsequent destruction by catalase does not diminish the response appreciably.

713. Watanabe, Takahide and Takao Nakamura (1980). Bioluminescence and Cell Growth of *Photobacterium phosphoreum*. *J. Biochem.* 88:815-817.

The bioluminescence activity of *Photobacterium phosphoreum* was compared at different times after cell division by the methods of density gradient centrifugation and synchronous culture. The bioluminescence intensity per cell mass increased linearly at a rate of 1.5 times per doubling time. The

luciferase system in the cell is continuously activated during growth, independent of cell division.

714. Waters, Paul and David Lloyd (1985). Salt, pH and Temperature Dependencies of Growth and Bioluminescence of Three Species of Luminous Bacteria Analysed on Gradient Plates. *J. Gen. Microbiol.* 131:2865-2869.

Two-dimensional diffusion gradients (of NaCl and H<sup>+</sup> concentrations) were established in a solid growth medium containing glycerol and yeast extract as major carbon sources. These were used to investigate conditions favorable for growth and bioluminescence of three species of luminous bacteria during incubation at different temperatures. *Photobacterium leiognathi*, *Photobacterium phosphoreum* and *Vibrio fischeri* all grew over the entire salt range used [0.9-3% (w/v) NaCl] and at pH values <7 at the most favorable temperatures (20°C, 2°C and 15°C, respectively); upper and lower temperature limits for growth over a 72-hour period were 30°C and 10°C, 25°C and 5°C, and 30°C and 5°C respectively. Bioluminescence was observed at all temperatures that supported growth; in *P. leiognathi* emission at 10°C was hardly detectable even after 72 hours, but at higher temperatures it occurred at all NaCl concentrations. Low pH values and high NaCl concentrations favored luminescence in the other two organisms; after 48 hours light emission decreased from the high pH and low NaCl regions of the gels. These results are discussed with reference to the symbiotic (*P. leiognathi*, *V. fischeri*) or free-living (*P. phosphoreum*) origins of the organisms studied.

715. Wecher, Richard A. and Ralph J. Bushnell (1981). Luminescent Oscillations in Microaerobic Batch Cultures of *Photobacterium phosphoreum*. In *Bioluminescence and Chemiluminescence: Basic Chemistry and Analytical Applications*, Marlene A. DeLuca and William D. McElroy, eds., New York: Academic Press, pp. 763-769.

Asynchronous batch cultures of *Photobacterium phosphoreum* grown under microaerobic conditions exhibited oscillations in light emission that did not correlate with culture growth or luciferase content, which increased steadily. The amplitude and frequency of the oscillations decreased with culture age. In cultures grown in unlimited oxygen less pronounced, short oscillations appeared only during the logarithmic

growth phase. Possible mechanisms to explain these oscillations are discussed.

716. White, Harris H. (1979). Effects of Dinoflagellate Bioluminescence on the Ingestion Rates of Herbivorous Zooplankton. *J. Exp. Mar. Biol. Ecol.* 36:217-224.

Ingestion rates of *Acartia tonsa* (Dana) on highly luminescent cultures of *Gonyaulax excavata* (Braarud) Balech are reduced by 50-75% relative to cultures with low capacity for luminescence. The effect is particularly noticeable at high cell concentrations. It is suggested that the dense array of flashes surrounding an animal disrupts its swimming and or feeding patterns. The activity of *Acartia clausi* at a density of 1 animal/3 mL stimulates 1.1% of the cells' capacity for luminescence each minute. *Pseudocalanus minutus* stimulates only 0.03% per minute, except in rare cases where the animals appear to be much more active. Cirripede and copepod nauplii never stimulate any emission. Favorable conditions for bioluminescence may arise before or during a bloom and the consequent reduction in grazing may contribute to maintenance of the bloom. Natural concentrations of zooplanktonic organisms cannot exhaust the bioluminescence of healthy *Gonyaulax excavata* cells.

717. Widder, Edith A. (1982). Effector Control of the Bioluminescent Dinoflagellate, *Pyrocystis fusiformis* (Murray). Ph.D. Dissertation, University of California, Santa Barbara.

In the marine dinoflagellate, *Pyrocystis fusiformis*, bioluminescence can be stimulated mechanically only during scotophase and exhibits a wide range of amplitude and kinetics in flashes. Previously unstimulated cells exhibit a first flash of about 200 msec duration, with a 10 msec rise time and biphasic decay. Subsequent flashes exhibit 500 msec durations, with 150 msec rise times and monophasic decays. First-flash kinetics can be recovered in 30-60 min in unfatigued cells or more than 6 hours in fatigued cells. During the first flash, the luminous microsources within the cell flash synchronously; subsequently they flash asynchronously. Submaximal stimulation produces a localized flash response.

718. Widder, Edith A., S. A. Bernstein, James F. Case and Bruce H. Robison (1986). Bioluminescence Patchiness, Scaling and Background Based on Image

Analysis of Video Recordings from a Midwater Submersible. *EOS* 67(44):994.

**ABSTRACT.** Bioluminescence stimulated by a 5 mm mesh screen was recorded at depths of 100 to 560 m in Monterey Canyon, CA, using an ISIT video camera mounted in the untethered, single person submersible Deep Rover. High bioluminescence potential and both horizontal and vertical patchiness were seen at all depths. Image analysis of the video recordings was used to quantify bioluminescence potential in terms of numbers and sizes of luminescent sources per m<sup>3</sup>. A high proportion of gelatinous sources which disintegrated on contact with the screen suggests that many present measurements of bioluminescence potential may be serious underestimates. A total absence of spontaneous bioluminescence was seen.

719. Widder, Edith A. and James F. Case (1980). Subcellular Basis for Two Flash Forms in a Bioluminescent Dinoflagellate, *Pyrocystis fusiformis*. *Amer. Zool.* 20(4):850.

**ABSTRACT.** The first flash of mechanically stimulated single cells of *Pyrocystis fusiformis* in scotophase is much brighter and exhibits faster kinetics than subsequent flashes. These different flash forms are a consequence of microsource coordination. During the first flash the microsources emit synchronously; subsequent flashes are asynchronous. This phenomenon is regional in the cell; that is, if only part of the cell responds to a localized stimulation, that part of the cell will respond asynchronously to subsequent stimulation, even though a previously unstimulated part of the cell will respond synchronously.

720. Widder, Edith A. and James F. Case (1981). Two Flash Forms in the Bioluminescent Dinoflagellate, *Pyrocystis fusiformis*. *J. Comp. Physiol.* A143:43-52.

A method was developed for studying bioluminescent activity in single cells of the dinoflagellate, *Pyrocystis fusiformis*. Individuals were isolated in holding tubes in day phase and held without stimulation until bioluminescence was maximally excitable, between circadian time (CT) 14 and CT 22, where CT 0 designates daybreak. Mechanical stimulation, via a pulse generator controlled solenoid, was applied to individual cells that had received no prior excitation in the night phase

tested. Two different flash forms were recorded. The first flash (FF) in response to a mechanical stimulus was very bright and had a rise time of 10 msec and a biphasic decay that was 90% complete approximately 200 msec from flash onset. The form of subsequent flashes in response to further stimuli differed radically from the FF. They were dimmer and longer lasting than the FF with approximately 150 msec rise times and a monotonic decay that was 90% complete as long as 500 msec from flash onset. Cells responded with one flash per mechanical stimulus and recordings were made until the response was exhausted. Total mechanically stimulated luminescence (TMSL) was measured with a digital integrator. TMSL and the integral of the FF were functions of cell size. The degree of potentiation and number of flashes per cell were functions of stimulus frequency. At higher stimulus frequencies cells produced fewer flashes and more light per flash. The effects of potentiation were long lasting, persisting for stimulus intervals of up to one minute. At slow stimulus frequencies (one pulse per 48 sec) bioluminescent activity was not totally exhausted during the 8 hours night-phase test period. With prolonged stimulation a fatigued flash form developed that combined elements of the FF and subsequent flashes. Cells that were stimulated to exhaustion recovered some bioluminescent capacity once stimulation ceased. Initial recovery was rapid and cells stimulated after only a 15 min recovery period produced as many flashes in the second stimulus series as in the first even though TMSL was reduced 82%. Therefore, the number of flashes a cell produced was not simply proportional to the amount of bioluminescent material available. The unique FF kinetics recovered with time, requiring 30–60 min in unfatigued cells and more than 6 hours in fatigued cells. With a 24-hour recovery period FF kinetics were more dependent on the cell receiving a normal 12-hour day phase than was TMSL recovery. Mechanically triggered bioluminescence in *Pyrocystis fusiformis* appeared to be the result of at least two temporally distinct processes, one of which was dependent on a precharging period.

Single cells of *Pyrocystis fusiformis* are excited mechanically by a piezo-electric crystal and chemically by acid and the propagation of the impulse across the cell is observed by image intensification techniques. A first flash, much more rapid and intense than any subsequent flashes, is observed. It is theorized that this is due to the synchronous discharge of the luminous microsources, which subsequently discharge asynchronously. When trains of mechanical pulses of varying intensities are used, both facilitation and fatigue are observed in individual cells. Synchronous and asynchronous flashing can occur simultaneously in different parts of the cell.

722. Widder, Edith A. and James F. Case (1982). Luminescent Microsource Activity in Bioluminescence of the Dinoflagellate, *Pyrocystis fusiformis*. *J. Comp. Physiol.* A145:517–527.

The basis for the different bioluminescent flash forms previously described in *Pyrocystis fusiformis* was examined using image intensification and microphotometric analysis. The unique kinetics (10 msec rise time and biphasic decay) of the first flash (FF) from a mechanically stimulated night phase cell resembled the kinetics of light emission from the individual microsources (microflashes). Synchronous light emission by microsources during the FF was replaced by their asynchronous flashing during subsequent flashes (SFs). Microsource kinetics changed to a skewed, bell-shaped microflash with a 40 msec rise time. The whole cell flash (macroflash) was of similar form but had slower kinetics than the microflash due to the asynchronous summing of microflashes, resulting in the 150 msec rise time characteristic of SFs. All microsources appeared to flash during the FF. Microsource emission during SFs was temporally unpredictable. A given microsource might or might not flash during an SF and could flash several times per stimulus. The dimness of SFs immediately following the FF resulted from a decrease in the number of active microsources. Potentiation of SFs with stimulus intervals of 1 min or less involved increasing numbers of active microsources. Fatigue occurred as a result of decreasing numbers of active microsources and decreasing microflash emission strength. Submaximal mechanical stimulation produced localized luminescent activity. Microsources responded as with maximal stimuli: initially with FF kinetics and synchrony, followed by SF kinetics and asynchrony.

721. Widder, Edith A. and James F. Case (1981). Bioluminescence Excitation in a Dinoflagellate. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis, (Minnesota): Burgess Publishing Co., pp. 125-132.

At frequencies of 0.33 pps and faster, the area of local luminescent activity enlarged with each stimulus, causing microsources in the new region of activity to respond as with an FF while the previously stimulated microsources exhibited SF kinetics and asynchrony. The long-term glow produced by acid-stimulated cells resulted from prolonged asynchronous activity of the microsources. Acid-stimulated microflashes displayed SF kinetics even with the first flash of a microsource. Recovery of FF kinetics occurred with a transition from asynchronous to synchronous coordination that was almost complete after 6 min. The transition from SF to FF microflash kinetics required longer recovery and was not abrupt, but exhibited intermediate kinetics. A model is presented as a guide to further study of bioluminescence control in this dinoflagellate.

723. Widder, Edith A. and James F. Case (1982). Distribution of Subcellular Bioluminescent Sources in a Dinoflagellate, *Pyrocystis fusiformis*. *Biol. Bull.* 162(3):423-448.

*Pyrocystis fusiformis* exhibits rhythmic changes in the distribution and mechanical excitability of subcellular bioluminescent sources. Bioluminescence in night-phase cells can be stimulated either mechanically or by low pH and originates from microsources found throughout the cytoplasmic layer surrounding the large central vacuole. Microsources are weakly fluorescent and probably correspond to 0.5  $\mu\text{m}$  or smaller cytoplasmic inclusions. With the onset of day phase, bioluminescence becomes mechanically inexcitable but responds to acid stimulation. Microsources disappear from the cell periphery during early day phase and all luminescence originates from the perinuclear region. In late day phase, bioluminescence originates both from the perinuclear region and from microsources in the periphery. However, luminescence remains mechanically inexcitable until the onset of night phase. Cells maintained in darkness exhibit the same rhythmic changes in mechanical excitability and development and disappearance of the perinuclear luminescence, except that microsources do not disappear from the periphery of early day-phase cells without a light induction period. Mechanisms which might underlie the rhythmic changes in bioluminescence distribution and mechanical excitability are proposed.

724. Widder, Edith A., Michael I. Latz and James F. Case (1983). Marine Bioluminescence Spectra Measured with an Optical Multichannel Detection System. *Biol. Bull.* 165(3):791-810.

The emission spectra of 70 bioluminescent marine species were measured with a computer-controlled optical multichannel analyzer (OMA). A 350 nm spectral window is simultaneously measured using a linear array of 700 silicon photodiodes, coupled by fiber optics to a microchannel plate image intensifier on which a polychromator generated spectrum is focused. Collection optics include a quartz fiber optic bundle which allows spectra to be measured from single photophores. Since corrections are not required for temporal variations in emissions, it was possible to acquire spectra of transient luminescent events that would be difficult or impossible to record with conventional techniques. Use of this system at sea on freshly trawled material and in the laboratory has permitted acquisition of a large collection of bioluminescence spectra of precision rarely obtained previously with such material. Among unusual spectral features revealed were organisms capable of emitting more than one color, including: *Umbellula magniflora* and *Stachytilum superbum* (Pennatulacea), *Parazoanthus lucificum* (Zoantharia) and *Cleidopus gloria-maris* (Pisces). Evidence is presented that the narrow bandwidth of the emission spectrum for *Argyrolepecus affinis* (Pisces) is due to filters in the photophores.

725. Widder, Edith A., Michael I. Latz and Peter J. Herring (1986). Temporal Shifts in Bioluminescence Emission Spectra from the Deep-Sea Fish, *Searsia koefoedi*. *Photochem. Photobiol.* 44(1):97-101.

The luminescence of freshly collected exudate from the post-cleithral organ of the deep-sea searfish, *Searsia koefoedi*, was increased in intensity by the addition of  $\text{H}_2\text{O}_2$  and exhibited emission maxima at 408 nm and 478 nm. Initially, the spectrum was unimodal with a long wavelength peak and a short wavelength shoulder. With time, the short wavelength peak increased in relative magnitude; the spectrum became bimodal, then the short wavelength peak predominated. The measured time-dependent changes in the spectral distribution resulted from differences in the rates of decay of the two peaks. The short wavelength peak exhibited first order exponential

decay with a mean ( $\pm$  standard deviation) decay constant of  $-0.13 \pm 0.02 \text{ min}^{-1}$  ( $N=4$ ). Decay of the long wavelength peak proceeded approximately twice as fast and was best defined by a double exponential function.

726. Widder, Edith A., Michael I. Latz, Peter J. Herring and James F. Case (1984). Far Red Bioluminescence from Two Deep-Sea Fishes. *Science* 225:512-514.

Spectral measurements of red bioluminescence were obtained from the deep-sea stomiatoid fishes *Aristostomias scintillans* (Gilbert) and *Malacosteus niger* (Ayres). Red luminescence from suborbital light organs extends to the near infrared, with peak emission at approximately 705 nm in the far red. These fishes also have postorbital light organs that emit blue luminescence with maxima between 470 and 480 nm. The red bioluminescence may be due to an energy transfer system and wavelength-selective filtering.

727. Wiebe, P. H., S. H. Boyd, B. M. Davis and J. L. Cox (1982). Avoidance of Towed Nets by the Euphausiid *Nematoscelis megalops*. *Fish. Bull.* 80(1):75-90.

Avoidance of towed nets by the common oceanic euphausiid crustacean, *Nematoscelis megalops*, was studied by comparing aspects of its sampling distribution as revealed by day and night catches of two nets of different size, one with a 1 m<sup>2</sup> mouth opening and one with a 10 m<sup>2</sup> opening. Both nets yield essentially the same pattern in vertical distribution. Paired tows yield a highly significant agreement in nighttime abundance estimates, but do not give comparable daytime estimates. Night catches, especially with the smaller net, exceed day catches, an effect which is interpreted as resulting from greater avoidance during the day. Comparisons between nets show that neither size net has a superior catch rate, day or night. No particular size group of the species is caught with greater efficiency by either net. When *N. megalops*' center of distribution is shallower, differences between day and night catches can be substantially enhanced. Application of Barkley's avoidance theory indicates that the potential advantage of greater mouth area of the larger net is effectively cancelled by individuals reacting to the approach of the net at a greater distance. Other theoretical predictions which depend upon the assumption of

increasing escape velocities as a function of body size are not corroborated by the field data. Thus, field population size-frequency distributions are probably not materially affected by avoidance. The evidence suggests that *N. megalops* uses vision to detect the net approach. Net contrast with the background due to downwelling light during the day and bioluminescence produced in and around the net both day and night appear to be the most likely stimuli. Future efforts to reduce net avoidance by species like *N. megalops* must focus on reduction of these signals.

728. Wilkens, Lon A. and Jerome J. Wolken (1981). Electroretinograms from *Odontosyllis enopla* (Polychaeta; Syllidae): Initial Observations on the Visual System of the Bioluminescent Fireworm of Bermuda. *Mar. Behav. Physiol.* 8(1):55-66.

In the waters of Bermuda, spawning of the polychaete annelid, *Odontosyllis enopla*, is intriguing due to the brilliant bioluminescent displays and lunar periodicity characteristic of the mating behavior. At 50-55 minutes after sunset, 2-5 days after the full moon, females become luminescent at the surface and thereby attract males for synchronizing the release of gametes. Previous studies have shown that bioluminescence in this species is maximal in the green portion of the visible spectrum ( $\lambda_{\text{max}}$  from 504-507 nm). The eyes of *Odontosyllis* exhibit maximum ERG amplitudes to green light as well ( $\lambda_{\text{max}}$  at around 510-520 nm), as determined by electroretinogram recordings made in response to light stimuli at various wavelengths. Color sensitivity in the eyes of *Odontosyllis* would therefore appear to be appropriate for sensing bioluminescent mating signals. Otherwise, the electroretinogram is a cornea-negative, monophasic potential of up to 8.0 mV in amplitude. Positive waveforms can be recorded away from the corneal surface near the midline of the head. Sensitivity is maximum for illumination along the optical axes of the four eyes, the direction of which is different for the anterior and posterior pair.

729. Wölken, Jerome J. (1984). Visual Sensitivity and the Eye Structure of the Fireworm *Odontosyllis enopla*, Bermuda. *Photochem. Photobiol.* 39(Suppl.):62S.

**ABSTRACT.** The marine annelid polychaete *Odontosyllis enopla* from Bermuda exhibits a lunar periodicity during the mating period accompanied by bioluminescence. The maximal visual spectral response

coincides closely with the maximum bioluminescence emission wavelength of 507–516 nm. Rods, possibly acting as fiber optic bundles, arranged in linear arrays, are associated with the photoreceptors. Such a fiber optic system would maximize the light-collecting ability of the eye and would function to detect the direction of bioluminescent emissions.

730. Wölken, Jerome J. (1986). Bioluminescence. In *Light and Life Processes*. New York: Van Nostrand Reinhold Co., pp. 215-224.

A brief historical discussion of bioluminescence research is presented. Bioluminescence in the coelenterates *Aequorea* and *Renilla*, the ostracod crustacean *Cypridina*, the dragonfish *Idiacanthus* and the polychaete worm *Odontosyllis*, is described in minimal detail. Photophores and their enervation in various organisms are depicted in general terms. Theories on the evolution of bioluminescence are outlined.

731. Wölken, Jerome J. and Robert G. Florida (1984). The Eye Structure of the Bioluminescent Fireworm of Bermuda, *Odontosyllis enopla*. *Biol. Bull.* 166(1):260–268.

The polychaete annelid, *Odontosyllis enopla* Verrill of the family syllidae in the waters of Bermuda, possesses a lunar periodicity and bioluminesces during the mating period. *Odontosyllis* has four eyes arranged so that two are located on each side of its head. The eyes are situated on lobes that have some degree of movement. Light sensitivity is maximum for illumination along the optical axis, which is different for the anterior and posterior pairs. The eye resides in a cavity formed by the pigment granules, and is structured of a lens, photoreceptor cells, the retina, and pigment granules. The retinal photoreceptors approach and surround the lens. The photoreceptors are formed of membranous processes, lamellae, and are similar in structure to the rhabdomeric photoreceptors of arthropods, cephalopod mollusc eyes, and the retinal rod outer segment of vertebrate eyes. The lens is a spheroidal body composed of cells. Closely associated with the lens are rods (tubes) about 60 nm in diameter arranged in linear arrays, suggesting that they are fiber optic bundles. The function of the fiber optic system could be to detect the direction of the bioluminescent light and to maximize the light-collecting ability of the eye.

732. Wroblewsky, Joseph S. (1986). Ocean Basin Scale Modeling of Plankton Dynamics and Bioluminescence in the North Atlantic. *EOS* 67(44):972.

**ABSTRACT.** Mathematical equations describing marine plankton dynamics have been solved for climatological conditions in the North Atlantic in May and surface layer distributions of phytoplankton, zooplankton and nutrients have been predicted as a function of historic mixed layer depth and the vertical gradient of dissolved nutrients. Model solutions of the phytoplankton field have been compared to CZCS chlorophyll images. Simulated light extinction coefficients at 490 nm have been compared to satellite-derived estimates.

733. Wyatt, Timothy (1979). Global Patterns of Discolored Water and Related Events in the Nineteenth and Twentieth Centuries. In *Toxic Dinoflagellate Blooms*. Dennis L. Taylor and Howard H. Seliger, eds., New York: Elsevier/North Holland, pp. 263-268.

Luminous phenomena do not necessarily correlate with discolored water. High concentrations of displays occur in the Gulf of Guinea, the Arabian Sea and the China Sea including the Gulf of Thailand. Luminescent eruptions and milky seas in the Indian Ocean are described. Milky seas are linked with the latter half of the southwest monsoon and both are linked with the new moon.

734. Wyatt, Timothy (1987). They Moved in Tracks of Shining White. *J. Cons. Inst. Explor. Mer* 44:56–58.

It is suggested that oceanic solitons may be responsible for some rare bioluminescent events recorded by merchant ships. A soliton is a kind of solitary wave which has some properties analogous with those of elementary particles.

735. Yamada, Kazuo, Margo G. Haygood and Hiroshi Kabasawa (1979). On Fertilization and Early Development in the Pine-cone Fish, *Monocentris japonicus*. *Ann. Report Keikyu Aburatsubo Marine Park Aquarium* 10:31–38 (Japanese).

*Monocentris japonicus* eggs were artificially fertilized and their development was observed for a period of 21 days. The larvae were fed *Brachionus* and *Artemia* nauplii, which were observed in the gut.

Neither luminous organs nor light emission could be observed in the young fish. The larvae reached a maximum total length of 6 mm. Fully developed *M. japonicus* juveniles resembling the adult as small as 11.0 mm in length have been reported.

736. Yang, Yikong, Lee pen Yeh and F. Tang (1980). The Isolation, Cultivation, and Identification of Luminous Bacteria. *J. East China Normal Univ.* 3:87-92. (Chinese).

This paper was not available for review.

737. Yang, Yikong, Lee pen Yeh, Yunhiu Cao, Linda Baumann, Paul Baumann, Jane Sung-en Tang and Blaine Beaman (1983). Characterization of Marine Luminous Bacteria Isolated off the Coast of China and Description of *Vibrio orientalis* sp. nov. *Current Microbiol.* 8:95-100.

Luminous strains of marine bacteria, isolated off the Coast of China, were subjected to a phenotypic characterization, which included a test of their ability to utilize 82 organic compounds as sole or principal sources of carbon and energy. A numerical analysis of the data revealed five clusters which were readily identified as *Photobacterium phosphoreum*, *P. leiognathi*, *Vibrio harveyi*, and *V. splendidus* biotype I. The remaining cluster of luminous isolates was phenotypically distinct from all the previously described species of *Vibrio* and *Photobacterium* and was given the species designation, *Vibrio orientalis*. This species differed from all the other luminous species of *Vibrio* by its ability to accumulate poly- $\beta$ -hydroxybutyrate as an intracellular reserve product. Additional distinctive properties were the presence of an arginine dihydrolase system, growth at 4°C but not 40°C and the ability to utilize putrescine and spermine.

738. Yentsch, Clarice M., Judith Dorsey, Sara Mayo and Colleen McKenna (1987). Metabolic Vigor and Bioluminescence Potential: Exploitation of Cytochemistry and Immunochemistry for Near Real-Time Characterization of Phytoplankton at Sea. *EOS* 68(50):1713.

**ABSTRACT.** Flow cytometry presently can accomplish automated enumeration, cell volume sensing and discrimination of various subpopulations of pigment/functional groups of phytoplankton on individual particles at sea in near real-time. It is proposed to extend these techniques to discriminate

between living and dead cells and to detect cells of bioluminescence potential. The latter can be accomplished by use of a fluorescently-labelled antibody to luciferase, which has been produced and used for laboratory testing of the concept.

739. Yetinson, T. and M. Shilo (1979). Seasonal and Geographic Distribution of Luminous Bacteria in the Eastern Mediterranean Sea and the Gulf of Elat. *Appl. Environ. Microbiol.* 37(6):1230-1238.

Luminous bacteria in the Mediterranean Sea and the Gulf of Aqaba-Elat have different distribution patterns. In the Mediterranean Sea, *Beneckea harveyi* is present all year round, with different subtypes alternating in summer and winter; *Photobacterium fischeri* was only present during the winter. In the Gulf of Elat, *P. leiognathi* is present throughout the water column in similar densities during the entire year. This constancy in distribution is presumably due to the near-constancy in water temperature. In summer, *Photobacterium leiognathi* is replaced by *B. harveyi* in coastal surface waters. In the hypersaline Bardawil lagoon, only *B. harveyi* types are present. *P. fischeri*, a major component of the Mediterranean Sea winter communities, is absent from the lagoon. Luminous *Beneckea* strains show a great diversity in properties, e.g., temperature range for growth, sensitivity to infection by phages, sensitivity to attack by *Bdellovibrio* strains, and difference in tolerance to high-salinity shock. Therefore, subdivision of the taxonomic cluster of *B. harveyi* into subtypes is indicated. The composition of the luminous bacteria communities may serve as indicators of different marine water bodies. The symbiotic luminous bacteria of the light organ of the common Gulf of Elat fish, *Photoblepharon palpebratus steinitzi*, is different from any of the types described.

740. Young, Richard E. (1981). Color of Bioluminescence in Pelagic Organisms. In *Bioluminescence: Current Perspectives*, Kenneth H. Nealson, ed., Minneapolis (Minnesota): Burgess Publishing Co., pp. 72-81.

Spectral measurements of bioluminescence in numerous marine species are summarized from reported literature and compared to absorbance maxima of visual pigments of mesopelagic species and spectral irradiance curves of moonlight and sunlight in the ocean and transmittance values for Jerlov Type I surface water.

741. Young, Richard E. (1983). Oceanic Bioluminescence: An Overview of General Functions. *Bull. Mar. Sci.* 33(4):829-845.

In the clear, dimly lit waters of the open ocean, nearly all of the larger inhabitants utilize luminescent structures. While the functions of bioluminescence vary greatly, luminescent organs are used primarily as major weapons of offense and/or defense in most of these animals. The bioluminescent systems used by oceanic organisms can be extremely sophisticated. For example, counterillumination systems have extremely complex physiological mechanisms, while luminescent flashes and clouds which may be used in a variety of ways involve highly complex behavioral mechanisms. In these waters, a bright luminescent signal may easily be detected and localized at considerable distance and often from any direction. While a widely broadcast signal may be advantageous in attracting prey or mates, the vulnerable sender may also expose its precise location to a hungry onlooker. Because luminescent displays are highly visible and because the users lack the protection of solid objects (e.g., rocks for hiding behind) in the open ocean, nearly every luminescent display carries with it some degree of risk. As a result, bioluminescence must be used with caution. The factors that shift the balance between advantage and disadvantage in a luminescent display are complex.

742. Young, Richard E. and John M. Arnold (1982). The Functional Morphology of a Ventral Photophore from the Mesopelagic Squid, *Abraia trigonura*. *Malacologia* 23(1):135-163.

The vertically migrating squid, *Abraia trigonura*, has at least two types of photophores involved in counterillumination. The most complex of these is described. They suggest that this photophore functions in the following manner. Innervated photocytes which contain crystalloids extract a component of the luminous reaction, presumably luciferin, from blood vessels via numerous finger-like processes. Energy for the reaction is supplied by banks of mitochondrial cells. Light is emitted by the crystalloids which are stacked to form a photogenic cone. The photogenic cone lies at the focus of a spherical proximal reflector. This reflector is an interference structure that selectively reflects light outward and contributes to color regulation by the alteration of its reflectance characteristics through changes in the diameter of its collagen rods. An

interference filter, the axial stack, selectively transmits light and contributes to color regulation by altering the thickness of the fluid-filled spaces between its platelets. The torus and distal cap are "thick film" reflectors that slightly diffuse the highly directional emission beam. Another interference structure, the distal reflector, reflects outwardly light emitted between the distal cap and the proximal reflector. Numerous chromatophores can conceal the photophore or aid in adjusting the radiance pattern of emitted light. The intensity of emitted light can be regulated over at least a 325-fold range, and the spectral emission maximum can vary between 480 and 536 nm. The angular distribution of emitted light can be regulated as well, but measurements have not been attempted. The photophore can rock on a fluid cradle which enables proper orientation regardless of the squid's attitude in the water. The complexity and the alterability of the light emission properties of this photophore, in combination with one or two other types of photophores, indicate that this squid can match many of the varying patterns of intensity, color, and radiance of downwelling light encountered in its oceanic habitat and, thereby, conceal itself by eliminating its silhouette from potential visual predators.

743. Young, Richard E. and John M. Arnold (1982). Photophore Regulation for Counterillumination in a Midwater Squid. In *Bioluminescence in the Pacific*, I. I. Gitel'zon and J. W. Hastings, eds., Krasnoyarsk: Akad. Nauk USSR, pp. 123-126.

The squid *Abraia trigonura*, which migrates from a preferred depth of 500-600 m during the day to less than 100 m at night, is found to regulate the intensity of its light emission from one type of photophore over a range of 300 fold. This probably represents less than 10% of its regulatory capability. It also can vary its peak emission wavelength from 480 nm to 536 nm and can alter the physical properties of parts of the photophore, a finding that suggests a capacity to control the angular distribution of the light.

744. Young, Richard E., Elizabeth M. Kampa, Sherwood D. Maynard, Frederick M. Mencher and Clyde F. E. Roper (1980). Counterillumination and the Upper Depth Limits of Midwater Animals. *Deep-Sea Res.* 27A:671-691.

The maximum counterillumination intensities of three species of mesopelagic squids and one species of mesopelagic fish were determined in a shipboard laboratory. The values were compared with the intensity of downwelling irradiance in the ocean measured off Oahu, Hawaii. The upper depth limits of the mesopelagic fauna were determined by midday and moonlit-night trawling. The data support the hypothesis that limits on concealment from predation through counterillumination determine the upper depth limits of this fauna during the day. At night near full moon, however, animals may be found at light levels higher than those at which counterillumination seems to be an effective strategy.

745. Young, Richard E. and Frederick M. Mencher (1980). Bioluminescence in Mesopelagic Squid: Diel Color Change During Counterillumination. *Science* 208:1286-1288.

Two species of mesopelagic squid greatly altered the color of their bioluminescence during counterillumination. The color change was triggered by changes in water temperature corresponding to those normally encountered by these vertically migrating animals. These squid can probably conceal themselves under the different colors of downwelling light that they encounter in their day and night habitats.

746. Young, Richard E., Clyde F. E. Roper and J. F. Walters (1979). Eyes and Extraocular Photoreceptors in Midwater Cephalopods and Fishes: Their Roles in Detecting Downwelling Light for Counterillumination. *Mar. Biol.* 51:371-380.

The means of detecting downwelling light for counterillumination in several midwater animals has been examined. Eyes and extraocular photoreceptors (dorsal photosensitive vesicles in the enoploteuthid squid *Abraliopsis* sp. B and pineal organs in the myctophid fish *Myctophum spirosum*) were alternately exposed to overhead light or covered by a small opaque shield above the animal and the bioluminescent response of the animal was monitored. Covering either the eyes or the extraocular photoreceptors resulted in a reduction in the intensity of counterillumination. Preliminary experiments examining the bioluminescent feedback mechanism for monitoring intensity of bioluminescence during counterillumination in the midwater squid, *Abralia*

*trigonura*, indicated that the ventral photosensitive vesicles are responsible for bioluminescent feedback.

747. Young, Richard E., R. R. Seapy, K. M. Mangold and F. G. Hochberg (1982). Luminescent Flashing in the Midwater Squids *Pterygioteuthis microlampas* and *P. giardi*. *Mar. Biol.* 69:299-308.

The luminescent flashing capabilities and swimming behavior were examined for two species of small midwater squids (*Pterygioteuthis microlampas* and *P. giardi*). Recently captured squid were placed in a small aquarium where their movements and luminescent flashes could be recorded with an image intensifier, a photomultiplier tube and associated equipment. Flashing behavior was initiated by disturbing the squid with an electrical shock. The following four behaviors were observed: (1) a short flash and a rapid departure from the electrode; (2) a short flash and a delayed, slow departure from the electrode; (3) a longer flash persisting after a rapid departure from the electrode; (4) a longer flash when departure was prevented by continuing the shock. Luminescent flashes probably have a general defensive function, discouraging or disrupting an attack by potential predators and within this context there may exist numerous strategies involving flashes.

748. Zavoruev, V. V., E. S. Vysotskii and V. V. Mezhevikin (1985). Photoinhibition of Luminescence of Phosphorescent Bacteria. *Microbiology (USSR)* 54(1):31-35 (Russian); 23-27 (English).

It was shown that visible light inhibits the luminescence of phosphorescent bacteria at intensities that do not damage the cells. The luminescence was inhibited most efficiently by light in the blue region of the spectrum. Light in the green and red regions had practically no effect on the luminescence. It is suggested that light acts either directly on the reduced natural analog of flavin mononucleotide, a substrate of bacterial luciferase, or on its reduction.

749. Ziegler, Miriam M. and Thomas O. Baldwin (1981). Biochemistry of Bacterial Bioluminescence. *Current Topics Bioenergetics* 12:65-113.

The biochemistry of the bacterial luciferase light-producing reaction, especially its stoichiometry, light-emitting molecule, and mechanism, is thoroughly discussed. Competing theories are presented and compared. Models are suggested for both the reaction

scheme itself and its place in the biological sequence of reactions in vivo. The structure of the molecule and its binding to various ligands are analyzed. The photoexcitation of luciferase is briefly mentioned. The nature and roles of the autoinducer, lumazine protein, and accessory enzymes are discussed in detail. The energetics of the reaction are considered.

750. Zinner, Klaus and Yelisetty Sree Vani (1987). Some Characteristics of the Bioluminescence of the Polychete, *Chaetopterus variopedatus*. Recent Results and Interpretations. *Bol. Fisiol. Anim.* (Sao Paulo)11:123-132.

Analysis of physical and chemical characteristics of the secreted mucus, together with the obtention from it of fluorescent low molecular weight molecules after the occurrence of the luminescent reaction and the study of iodine distribution (and possible coincidence with bioluminescent regions) along the body of the marine polychete worm *Chaetopterus variopedatus* are under way in connection with their possible participation in the bioluminescent phenomenon. Results obtained by employing several spectroscopic techniques, allied to direct visual and also autoradiographic observations tend to support their importance and apparently quite close interrelationship.

## ADDENDUM

The following articles were found too late to be included in the main body of abstracts. They are, however, fully indexed.

751. Aoki, T., T. Kitamura, S. Matsuno, K. Mitsui, Y. Ohashi, A. Okada, D. R. Cady, J. G. Learned, D. O'Connor, M. McMurdo, R. Mitiguy, M. Webster, C. Wilson and P. Grieder (1985). Background Light Measurements in the Deep Ocean. Institute for Cosmic Ray Research, University of Tokyo, Report ICR-123-85-4.

Ambient light intensities in the ocean at depths between 1500 m and 4700 m near Hawaii were measured around the one photoelectron level with 5" diameter hemispherical photomultipliers. Measurements of count rates above variable thresholds were carried out in ship suspended and bottom tethered configurations. The ship suspended rates show considerable fluctuation and their mean value decreases with depth approximately as

$\exp[-x(m)/877]$ . The bottom tethered rates are about an order of magnitude lower than the ship suspended rates and show little fluctuation. The calibration of our instrument indicates an absolute flux at 4700 m depth based on the bottom tethered measurement of  $218^{+20}_{-60}$  photons/cm<sup>2</sup> × s, which is consistent with calculated intensities due to b-decay electrons from <sup>40</sup>K. The difference in the two cases is attributed to bioluminescence due to environmental stimulation.

752. Arrio, Bernard, Alain Dupaix, Chantal Fresneau, Bernard L'cuyer, NicoleLescure and Pierre Vollin (1980). Purification de l'Emetteur de Fluorescence chez les Polynouinae (Annélides Polychètes). *Comp. Rend. Acad. Sci. Paris* (Ser. D) 290:1537-1540. (French).

The fluorescent emitter from the epithelial cells of the polynoid worms has been purified by gel chromatography. A peroxidasic mechanism is proposed to account for the bioluminescent reaction.

753. Baranova, N. A., V. S. Danilov and N. S. Egorov (1984). NADH-Dependent Luminescence and Efficiency of Luminescent Systems in Different Species of Marine Bacteria. *Microbiology* (USSR)53(6) :896-902 (Russian) :724-729 (English).

We have determined the activity of luciferase and the intensity of the NADH-dependent luminescence of enzyme preparations of three species of marine luminescent bacteria: *Photobacterium fischeri* MJ-1, *Beneckea harveyi* 392(MAV), and *Photobacterium phosphoreum* NZ-11D. We have shown that the NADH-dependent luminescence is not proportional to the activity of NADH:FMN oxidoreductase and luciferase, but depends on the ratio of these enzymes, the concentration of the substrates for the luminescent system, and the activity of the dark pathways of NADH oxidation. We have calculated the efficiency of theoperation of luminescent systems of the species studied and established that the highest efficiency of operation of the luminescent chain is shown by the *P. fischeri* culture. Therefore, this species is more suitable for use in the analysis of the NADP-dependent enzyme systems. We have concluded that the activity of luciferase, the NADH-dependent luminescence, and the ratio of the NADH-dependent luminescence to the activity of the luciferase can serve as one of the important species characteristics of the species of luminescent bacteria studied.

754. Bilbaut, André (1980). Cell Junctions in the Excitable Epithelium of Bioluminescent Scales on a Polynoid Worm: A Freeze-Fracture and Electrophysiological Study. *J. Cell Sci.* 41:341-368.

The bioluminescent scales of the polynoid worm *Acholoe* are covered by adorsal and ventral monolayer of epithelium. The luminous activity is intracellular and arises from the ventral epithelial cells, which are modified as photocytes. Photogenic and nonphotogenic epithelial cells have been examined with regard to intercellular junctions and electrophysiological properties. Desmosomes, septate and gap junctions are described between all the epithelial cells. Lanthanum impregnation and freeze-fracture reveal that the septate junctions belong to the pleated-type found in molluscs, arthropods and other annelid tissues. Freeze-fractured gap junctions show polygonal arrays of membrane particles on the P face and complementary pits on the E face. Gap junctions are of the P type as reported in vertebrate, mollusc and some annelid tissues. d.c. pulses injected intracellularly into an epithelial cell are recorded in neighbouring cells. Intracellular current passage also induces propagated nonovershooting action potentials in all the epithelial cells; in photocytes, an increase of injected current elicits another response which is a propagated 2-component overshooting action potential correlated with luminous activity. This study shows the coexistence of septate and gap junctions in a conducting and excitable invertebrate epithelium. The results are discussed in relation to the functional roles of intercellular junctions in invertebrate epithelia. It is concluded that the gap junctions found in this excitable epithelium represent the structural sites of the cell-to-cell propagation of action potentials.

755. Bilbaut, André (1980). Excitable Epithelial Cells in the Bioluminescent Scales of a Polynoid Worm: Effects of Various Ions on the Action Potentials and on the Excitation-Luminescence Coupling. *J. Exp. Biol.* 88:219-238.

The bioluminescent scales of the polynoid worm *Acholoe astericola* are covered with photogenic and nonphotogenic excitable epithelial cells which are electrically coupled. The luminescent activity is intracellular and occurs in brief flashes. All the epithelial cells produce nonovershooting action potentials which have been shown to be Na-dependent. In the photogenic epithelial cells (photocytes) the increase of the stimulus strength elicits another action

potential specifically correlated with a flash. This membrane response begins by a fast overshooting Ca-dependent spike potential followed by a Na-dependent secondary depolarization. The excitation-luminescence coupling is dependent on Ca entry into the photocytes.

756. Bradner, Hugh, Antares Parvulescu and Grant Blackinton (1980). Fast Bioluminescence Pulses in DUMAND. In *Proc. 1980 DUMAND Signal Processing Workshop*, A. Roberts, ed., Hawaii DUMAND Center, University of Hawaii, Honolulu, Hawaii, pp. 6-19.

The design for an instrument to measure bioluminescence flashes with rise times of 10-100  $\mu$  sec (instead of the usual one or more milliseconds) is proposed. Such an instrument is needed to test a model of mechanical stimulation that would result in the possibility of low-intensity submillisecond rise times, even though there is no evidence that they actually do occur. A mathematical analysis suggests that "quasi-steady" bioluminescent flashes (rise times on the order of milliseconds and durations on the order of hundreds of milliseconds or longer) and peak intensities at the detector of  $10^7$ - $10^{13}$  quanta  $\text{cm}^{-2} \text{sec}^{-1}$  (actual reported measurements) will completely mask Cerenkov events during the time of the flash, even if the photomultiplier output is time-gated to detect only short-term transients.

757. Engebrecht, JoAnne, and Michael Silverman (1986). Regulation of Expression of Bacterial Genes for Bioluminescence. In *Genetic Engineering: Principles and Methods*, J. K. Setlow and A. Hollander, eds., New York: Plenum Press, pp. 31-44.

The biochemistry of the bacterial bioluminescence reaction and its regulation by autoinduction are briefly described. All the necessary enzymatic functions are encoded on one DNA fragment, which contains five *lux* genes (*lux A*, *B*, *C*, *D* and *E*) and two regulator genes (*lux I* and *lux R*). A map of the DNA fragment is given. Autoinducer is found to function by regulating the transcription of *lux* genes in operon R (all *lux* genes except *lux R*). *Lux I* encodes a function for autoinducer synthesis while *lux R* controls the transcriptional response to autoinducer by producing a protein whose synthesis is repressed by autoinducer. Thus, *lux I* functions (via autoinducer) negatively to regulate expression of *lux R*

and prevent overproduction. A regulation model is presented, consisting of the existence of two genetic control circuits, both requiring *lux R* and *lux I* functions. One circuit is a positive feedback circuit that regulates transcription of operon R; the other is a negative feedback circuit that regulates expression of operon L (the *lux R* gene) at the translational level.

758. Jones, M. B., William W. Ward and Barbara A. Zilinkas (1979). Lucifer and the Capture of Light. *Matrix* 79(Winter):13-15.

The interactions of light and living organisms are discussed in terms of photosynthesis (the capture of light energy to produce chemically stored energy) and bioluminescence (the use of chemically stored energy to produce light). It is estimated that 95% of deep-water fish produce light. The functions of light production as a mating signal, to capture prey, and to defend against predation are described. The energetics of light production and energy transfer in some light-producing reactions are outlined.

759. Losee, Jon R. (1982). Bioluminescence in the Deep Ocean. In *Proc. DUMAND 1982 Signal Processing Workshop*. A. Roberts, ed., Hawaii DUMAND Center, University of Hawaii, Honolulu, Hawaii, pp. 19-29.

Observations of bioluminescence using dark-adapted eyes and a low-light-level SIT video camera on a series of dives on the deep submersible Trieste in July-August 1977 to 2500 m and 1979 to 3650 m in the Gulf Stream off North Carolina and on a series of dives on the submersible Alvin in July-August 1980 at or near the Woods Hole Deep Ocean Site II (also in the Gulf Stream off North Carolina) to a maximum depth of 3650 m are presented. The detector is described. On the Alvin dives, sunlight masked bioluminescence to a depth of 380 m. Fragile stringy gelatinous organisms (thought to be siphonophores), ranging in size from 0.5 to 20 cm, were responsible for most of the observed light. Their fragility prevented successful sampling by midwater trawls. The bioluminescence count rate ranged from 10 to  $4 \times 10$  counts per second, with a large layer at 1100 m and smaller layers at 1500 m and 1800 m. A layer of UV bioluminescence was seen at 1500 m with some activity at 2200 m. No structure was seen in the temperature profile at these depths. The time structure of the signal was not uniform but occurred in sporadic bursts.

760. Nicolas, Marie-Thérèse (1979). Présence de Photosome dans les Fractions Lumineuses du Système Elytral des Polynoïnae (Annélides Polychètes). *Comp. Rend. Acad. Sci. Paris (Ser. D)* 289:177-180. (French).

After centrifugation on sucrose gradient of homogenized elytra of scaleworms, luminescent activity, with sodium dithionite, shows an unimodal distribution. The maximum response is obtained for a fraction, and only for this fraction, which contains characteristic photosomes.

761. Nicolas, Marie-Thérèse (1980). Solubilisation du Système Lumineux des Polynoïniens. Comparaison de Différents Tests d'Activité. *Biol. Cell.* 39:5a. (French).

**ABSTRACT.** Luminescence in polynoid worms in vivo is associated with membrane-bound photosomes. In vitro, luminescence co-migrates during gradient centrifugation with the photosome fraction as shown by three different activity tests. Activity is enhanced when the particulate fraction is solubilized using a nonionic detergent.

762. Primakova, G. A., T. P. Turova, V. V. Zavoruev and T. I. Vorob'eva (1983). Determination of the Taxonomic Position of *Photobacterium belozerskii*. *Microbiology (USSR)* 52(1):91-101 (Russian):82-85 (English).

On the bases of phenotypic analysis, kinetic characteristics of the luminescent reaction, and DNA-DNA hybridization, *Photobacterium belozerskii* is shown to be synonymous with *Benickeia harveyi*.

763. Stachnik, William J. (1986). The Simulation of Marine Light Fields Including Polarization and the Related Visual Behavior of *Mysidopsis bahia*. Ph. D. Dissertation, Yale University.

An apparatus has been constructed that allows the underwater marine light field to be physically simulated using artificial light sources and optical components. The arrangement of components allows downwelling, sidewelling, and upwelling marine light to be recreated in its measured or theoretically determined spectral and polarized structure. The design of an apparatus of this type takes into account a generalized set of simulation categories called simulation regimes. The visual parameters of the animal to be studied, the optical nature of the water to be simulated, and the depth in the water column selected, define a particular simulation regime category.

through the underwater contrast-visual range equation of Duntley and the geometrical criteria defined in this thesis. Two types of bioluminescence, daytime and nighttime, are considered as part of the Deep Benthic Regime. This work seeks to provide researchers with a means of investigating marine animal behaviors that utilize specific aspects of the spectral and polarized structure of marine light. Initial results of experiments performed with the apparatus, involving a nonluminous mysid shrimp, *Mysidopsis bahia*, are given to demonstrate the use and range of application of the apparatus.

764. Vorob'eva, T. I., Ye. S. Vysotskii, V. V. Zavoruev and V. V. Mezhevikin (1980). Regulation of Luciferase Synthesis in *Photobacterium mandapamensis*. *Microbiology (USSR)* 49(4):517-520 (Russian):452-455 (English).

Luciferase synthesis by the strain 54-K of *Photobacterium mandapamensis* during batch cultivation is not sensitive to an inhibitor in the growth medium and does not require accumulation of autoinducer. Since the intensity of luminescence and the luciferase content per cell do change, the bacterium seems to possess an additional system for regulating luciferase synthesis, independent of both inhibitor and autoinducer.

765. Ward, William W. (1979). Energy Transfer in Bioluminescence—A Yellow Tryptic Peptide from the Green-Fluorescent Protein. *Abstr. Int. Cong. Biochem.* 11:160.

**ABSTRACT.** Green in vivo bioluminescence in the sea pansy *Renilla* involves an efficient, radiationless energy transfer reaction from an enzyme-bound excited state oxyluciferin molecule to a conjugated protein called the green-fluorescent protein (GFP). A similar system exists in the jellyfish *Aequorea*. A covalently-bound yellow chromophore, present in both GFP's, is responsible for the absorption and fluorescence observed in the visible spectral region. Yellow tryptic peptides have also been chromatographically isolated from both GFP's.

766. Zapata Fisheries Development Corporation (1980). Demonstration of Capability for Detection of Herring with Aerial Fisheries Survey System. Summary Report, Contract NA-79-FAC-00044 with the National Marine Fisheries Service.

An airborne low-light-level image-intensifying TV camera system was used successfully to detect schools of herring at night in the Gulf of Maine, Georges Bank and Nantucket Shoals during September–November 1979. Herring schools were identified and sized by their movement in reaction to stimulation by a flash from a light mounted beneath the aircraft. Little movement occurred without stimulation.

767. Zeitz-Nicolas, A. M., D. Thin's-Sempoux, G. Zurstrassen and Fernand Baguet (1980). Model of Cellular Mechanism of Bioluminescence in *Porichthys*. *Arch. Int. Physiol. Biochem.* 88(2):B118-B120.

Mitochondria usually dispersed in the cytoplasm of *Porichthys* photogenic cells coalesce around the photocytic vesicles and change in size and appearance during light emission. Exhausted photocytes have completely disorganized vesicles and membranes whereas stimulated photocytes that did not emit light continue to exhibit regularity in structure. It is therefore proposed that mitochondria play a central role in photogenesis by regulating  $Ca^{2+}$  concentration in the cytoplasm, probably by membrane loading and unloading, and that regularly coiled membranes of the coalesced vesicular pools are a prerequisite for the luminous reaction. A model sequence of intracellular events leading to light emission is proposed.

768. Zinner, Klaus, and Yelisetty Sree Vani (1986). Some Characteristics of the Mucus of the Bioluminescent Polychete, *Chaetopterus variopedatus*. *Bol. Fisiol. Anim.* (Sao Paulo)10:7-14.

The physical and chemical properties of the mucus of the bioluminescent polychete *Chaetopterus variopedatus* are being studied in connection with their close relation with the animal's bioluminescence. Two distinct fluorescent fractions are consistently being separated by molecular sieve filtration and analysed via spectrophotometric and spectrofluorimetric techniques. The emission fluorescence spectral distributions closely resemble that of the bioluminescent emission with maxima in the 460-480 nm region. Chromophore groups at ca. 320, 365, 395 and 420 nm seem to be present in both fractions, as shown by absorption and fluorescence excitation spectra, indicating their possible close relationship. At least two of these groups are charged, as shown by behaviour at different pH's.

## **Appendix B**

### **Author, Taxonomic, Geographic, and Key Word Indexes**

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#### **Author Index, p. 171**

The author index is organized alphabetically. In the case of translations from Russian, alternate spellings are sometimes given.

#### **Taxonomic Index, p.**

The taxonomic index is organized into major groupings to increasing complexity of the organisms involved. Within each grouping, the organisms are arranged alphabetically, first by genus, then species. The major groups are identified by their common name, then by the scientific classification (following abstract 277 in this bibliography). Abstract numbers given for the major groupings are for review papers that cover the entire group or for papers in which the organism studied was not further identified.

Only organisms on which original work was done in the article cited are included in the index, except for reviews. Nonluminous organisms are included in the index, if the possibility of their luminosity was considered by rejected conclusively, or if a statement was made to the effect that they were definitely nonluminous. However, terrestrial and fresh-water organisms mentioned were indexed, even if they are luminous, on the grounds that this is a bibliography of marine bioluminescence. Likewise, luminous organisms discussed in a context not relating to bioluminescence (e.g., toxicity of *Protogonyaulax tamarens*) have not been indexed. The letters "sp." after the name of a genus or higher taxonomic group designate either that the remarks in the article cited apply to all members of the group or that the organism discussed was not further identified.

#### **Geographic Index, p.**

The geographic index is organized first by major bodies of water (oceans or enclosed seas) arranged alphabetically. World-wide papers are last. Within each body of water more specific locations are arranged alphabetically.

#### **Key Words, p.**

The key words were chosen either directly from the paper cited or with consideration of naval interest.

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